COMPARATIVE PROPERTIES OF RIVERS AND LAKES FROM AN ONTARIO PERSPECTIVE

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In the past, aquatic ecologists in Ontario have directed most of their efforts to the study of lakes. These core studies now represent a mass of ecological information which, when extrapolated to other lakes, is useful for the management of their fisheries. Ontario rivers, on the other hand, have been routinely neglected until recently, with few exceptions. This neglect has led to the consideration of the transfer of information derived from a lake data base and applied to the management of river fisheries. The feasibility of such a transfer depends on the commonality shared by lakes and rivers, or the differences, as described herein. The tendency to consider rivers as a subset of lakes is tempting, particularly for the purpose of science transfer. However, real qualitative differences exist that make such transfers impractical, unless the differences are first accounted for. Differences between rivers and lakes may be aptly expressed in terms of six dichotomies, namely: space-time orientation; horizontal or vertical stratification; exogenous or endogenous environmental influence; allochthonous or autochthonous sources of energy and nutrients; relative levels of abiotic and biotic effects; and proportional distribution of autotrophic and heterotrophic production. Other important qualitative differences relate to morphology, hydrodynamics, temperature, chemistry, and biota. Rivers possess certain ecological peculiarities not found in lakes, or at least that are less significant there. These include the boundary layer, nutrient spiralling, the hyporheic zone, and various reset events.

Key words: rivers, lakes, morphology, hydrodynamics, temperature, chemistry, biota, ecological phenomena, communities

INTRODUCTION

During the early part of the past century, the science of aquatic ecology in Ontario has directed its most intensive efforts towards the study of lakes and their aquatic communities (e.g. Wright 1892; Bensley 1922; Clemens 1923; Dymond 1926). These studies have intensified with time (e.g. Martin and Olver 1976; Adams and Olver 1977), and over ever-increasing geographic areas, until today a formidable depth of ecological information exists for more than 10,000 lakes, in data files of a highly systematized and readily retrievable format (Ontario Fisheries Information System). While these files are not exhaustive *sensu stricto*, the individual lake studies are representative of a wide geographic area which will allow extrapolation with reasonable confidence, to other lakes within the Province that remain yet unsurveyed.[2] Generally speaking, information required for lake management in Ontario is easily accessed and appropriate to applications running from fisheries quota allocations to environmental rehabilitation. Accordingly, fisheries management strategies for Ontario lakes are supported by a vast and robust data base, and management personnel have the option of making ecologically sound decisions.

While increasingly intensive and significant effort (in terms of funding and human resources) has been directed towards the study of Ontario lakes over the last 70 years, it was accomplished at considerable sacrifice to river

[1]A concise version of this paper may be found in the Proceedings of the Large Rivers Symposium (LARS) issued as Can. Spec. Publ. Fish. Aquat. Sci. 99. 1988.

[2]There are something on the order of one quarter to one half million lakes in Ontario (Cox 1978), Canada's second largest province by area. To the best of our knowledge, statistics of this nature are not available for lotic systems in Ontario.

research. Ricker (1934) observed that large amounts of detailed information existed on Ontario lakes by the 1930s, resulting in various classification systems applicable throughout the north-temperate region. He also noted that rivers had been almost uniformly neglected, with but few exceptions. Today, more than 50 years later, lotic classification schemes remain enigmatic (e.g. Cushing et al. 1983). Ricker attributed this discrimination against river research to the presence of several logistic hurdles that had to be transcended before any useful syntheses could be made. Two examples included the need for a description of an overwhelming variety of habitats in rivers and a thorough systematic treatment of river fauna. A third consideration related to the neglect of rivers in Ontario was the fact that the potential economic importance of their fish populations was markedly lower than that of lakes. To this day, Ricker's 1934 treatise "An Ecological Classification of Certain Ontario Streams" remains the most complete, well-organized, and definitive ecological description and classification of Ontario's small rivers. Unfortunately, the geographic scope of that document was restricted to a rather small area of the southern part of the Province.

One might wonder at the inordinately great amount of attention paid to lakes by limnologists and fisheries biologists in a jurisdiction liberally laced with river systems. In addition to Ricker's (1934) observations, this inequity is at least partly derived from the disproportionately high ratio of lakes to rivers in the north-temperate zone as compared with the tropics (Fernando 1980). Consequently, significant treatises exist for tropical rivers and their fisheries (e.g. Welcomme 1979, 1985), but northern rivers occupying previously glaciated zones are but poorly documented, if at all. Accordingly, no clear unifying concepts have emerged pertaining to fish production and standing stocks in the north-temperate, previously glaciated, streams of North America. The excellent volume of Hynes (1970) on "The Ecology of Running Waters", a river document of global scope, remains to this day as the single best work applicable to these streams.

The disproportionate emphasis on lakes as opposed to rivers is not unique to Ontario, however, nor even to Canada. Huet (1959) noted a similar inequity between research in standing freshwaters such as lakes, ponds, and marshes, as compared with running waters in Western Europe. Apparently, pristine river systems have been particularly neglected worldwide (Statzner & Higler 1985). Welcomme (1979) also observed an imbalance between the available font of information existing for lakes as opposed to rivers, and suggested that only recently have comparable efforts been made in the area of river fisheries in some parts of the world. Perhaps this inequitable treatment of rivers stems from the fact that on a volumetric basis they constitute only 0.004% of the world's fresh waters (calculated from data presented in Vallentyne 1972).

Because of the inordinately high ratio of lakes to large rivers in Ontario as compared to the situation in the tropics (Fernando 1980), advancement in the development of techniques applicable to the study of rivers has suffered. Much of the sampling or capture gear useful in lentic environments is inefficient, or only marginally effective in a lotic milieu. Consequently, Nansen bottles and gill-nets may not be efficient for sampling in rivers, and most lake sampling gear becomes reduced in its quantifiable representiveness when used in a stream environment. As much of the new sampling gear based on hi-technology was originally designed and tested on oceans and then transferred to lake application (Kerr and Ryder 1988), its use on streams is often logistically difficult, and impractical.

Compounding these considerations is the general predilection of Canadian universities to train limnologists and fisheries biologists within a lake context. This situation likely occurs generally in Canada with some notable exceptions on the East and West Coasts, both of which have economically valuable anadromous fisheries. We know of no instance, however, where a curriculum in "rheology" is offered, which might specialize in the physical, chemical and biological attributes of running waters, and serve as an appropriate counterpart

to "limnology" for lakes. Similarly (with the possible exception of Hynes 1970), we are unaware of rheological treatises approaching the exhaustive treatment of limnology (e.g. Welch 1952; Hutchinson 1957, 1967, 1975; or Wetzel 1975 which are but three examples).

The insufficiency of physical, chemical and biological data for Ontario rivers likely stems from the fact that despite its position as the most populous province in Canada, and second in area only to Quebec, it has developed relatively small hydro-electric projects when compared with those of the James Bay drainages of Quebec, or the Churchill-Nelson River system in Manitoba. Furthermore, in Ontario, an inventory of streams and rivers exists only in rudimentary form, and principally for southern streams.

We have made the case for the relative dearth of information available pertaining to the physical, chemical and biological attributes of Ontario rivers, yet, at the same time, we note the existence of a highly organized and easily accessible information file for Ontario lakes. With the constraints of funding and limiting human resources, the ecological concepts and methodologies derived from lake sets might be seen as extended and applied to rivers under favourable circumstances. We have already alluded to the general inappropriateness of lake sampling methods when applied to rivers. Ecological concepts, however, if taken at a sufficiently fundamental level, may be equally applicable to either lakes or rivers. Ricker (1934) with remarkable prescience, suggested the possibility of extending to streams generally, the systematic ecological treatment already applied to lakes. The comparative approach among lakes, reservoirs and rivers has produced both interesting and informative ecological insights (e.g. Ryder 1978a; Regier and Henderson 1980). We intend to extend these insights to a comparison and contrast of large lakes and rivers of the world (e.g. Ryder and Pesendorfer 1988), with a perspective on application to a particular suite of large rivers in Ontario. We attempt this exercise within the context of the "River Continuum Concept" (Vannote et al. 1980; Minshall et al. 1985; Sedell and Richey 1988) and one of its logical extensions, the "Stream-Bay-Lake-Continuum" (Francis et al. 1985). Neither our topics (morphology, hydrodynamics, temperature, chemistry, trophodynamics, biota), nor our treatment, are intended to be exhaustive, but rather, to serve as a general entry into important facets of river ecology, and particularly, to provide an ecological foundation for future studies of fish production in large Ontario rivers.

DISTINGUISHING FEATURES

Rivers and lakes have many physical, chemical and ecological features that may be readily compared or contrasted. We have selected some of the most prominent attributes of both lotic and lentic systems, in order to demonstrate the fundamental differences or commonalities. This compare-and-contrast exercise focuses sequentially on morphology, hydrodynamics, temperature, chemistry and ecology. Much of the information presented in the text has been summarized in tabular and graphic form for ready comprehension. The perspective portrayed is, of necessity, that based upon the authors' previous experience, and is intended to provoke further insights into river ecology. Other perspectives derived from the same set of information may be equally valid.

MORPHOLOGY

Many morphological characteristics of rivers distinguish them from lakes (Table 1), although the typical river system embodies both lotic and lentic features (e.g. Moss 1980). River habitat as characterized by morphometry, is a dynamic, often ephemeral phenomenon, which is typified by seasonal and spatial changes (Leopold et al. 1964). Hynes (1970) suggested that a network of variables (discharge, width, depth, rate of flow, substrate resistance, and sediment transport) interact, undergoing constant adjustment, to achieve the existing river channel characteristics. The physical and hydrobiological features of a river are strongly inter-

Table 1. A comparison of morphological attributes, primarily for north-temperate rivers and lakes.[1]

Attribute	Rivers	Lakes
Channel or basin contours	Change spatially	Constant
Erosion/deposition ratio	Decreases downstream	Decreases from near shore littoral to greater depth
Shoreline erosion	Extensive, induced by water currents	Localized, induced by wind-driven waves
Mean particle size	Decreases downstream	Decreases with depth
Number of substrate types	Increases downstream	Determined by geomorphology and wave action
Distribution of substrate	Determined by water current; gravity driven	Determined by wind-induced currents
Mean depth	Low	High
Depth gradient	Increases from headwaters to mouth	Deepest remote from shore
Shape	Long, meandering, linear	Short, ovoid
Breadth/shoreline length ratio	Low	High
Watershed/surface area ratio	High	Low
Turbidity	High	Low
Ice formations	Transitory	Persistent
Ice scouring effects	Extensive	Localized to windward, near-shore littoral

[1]Data were derived in part from the following sources: Hynes 1970; Vannote et al. 1980; Statzner and Higler 1985.

related; for example, swiftly flowing water is typically associated with a stony substrate (Smith 1980), high elevations, and a propensity to frequent, fierce storm flows (Haslam 1978). As a result, the lotic ecosystem approaches a state of conservative dynamic equilibrium.

The morphological characteristics of a river change as its water moves from the source to the mouth; for example, the topography assumes a lower profile and the channel gradient generally decreases (Haslam 1978). The gradient from headwaters to the mid-reaches, and thence to the mouth, has been described as a "spectrum of differentially variable habitats" (Minshall et al. 1985). The gradient of a river dictates the direction and rate of flow; thus, it determines the course of a river. In addition, slope or gradient is usually indicative of the type of fish fauna present (Huet 1946, 1949; Hocutt and Stauffer 1975), as well as other taxa (Hynes 1970; Cummins and Spengler 1978). The channel generally widens and deepens in a downstream direction; however, channel width increases more rapidly than depth (Hynes 1970; Beaumont 1975; Haslam 1978). The ecological significance implicit therein is that within any given biogeographical area, rivers of comparable breadth, depth and slope exhibit faunal characteristics of great similitude (e.g. Huet 1959).

On the other hand, the basin morphology of lakes remains relatively stable, except for moderately small and localized effects caused by wind-induced waves and subsequent sedimentation (Table 1). This general characteristic of basin stability of lakes tends to promote a greater stability within their contained biotic assemblages, which may be described as less stochastic than those of riverine biota (e.g. Grossman et al. 1982).

Rivers integrate erosional and depositional habitats, the former typically occurring in sections where rapid flow prevails, often in the narrow, upper reaches, while deposition of silt and detritus occurs in regions of slow current (Shelford 1914; Shelford and Eddy 1929; Moon 1939; Statzner and Higler 1985). Banks of rivers may erode, shift, or form levees on one or both sides of the river, as has happened, for example, in some of the large rivers of the Hudson Bay lowlands. Material input and transport capacity must be in dynamic equilibrium if the stream bed is neither to erode, nor to accumulate debris or silt (Statzner and Higler 1985).

Overall, lakes are more stable physically and, in general, their shorelines are eroded more slowly than are the banks of rivers. While the causative factors in natural river bank erosion are primarily water current and changing water levels, shoreline erosion of lake shores is largely due to wind-induced waves (Table 1).

In the middle reaches of rivers, the gradient generally decreases to intermediate levels (Patrick 1972; Smith 1980). However, the current velocity may be slightly increased (Hynes 1970; Patrick 1972), and the silt load suspended by the water becomes greater (Patrick 1972). This stream region, transitional between erosional upper reaches and depositional lower reaches (Statzner and Higler 1985), is characterized by larger meanders than in the upstream reaches (Patrick 1972; Smith 1980). Because of their physical complexity, meanders tend to promote ecological diversity (e.g. MacArthur 1972), and a deeper stream results due to the resistance to flow (Hynes 1970). If channel sinuosity is low, limited bank cutting, few pools and a uniform cross-sectional profile are the consequences (Platts et al. 1983).

In the lower stream reaches the gradient flattens markedly, and sedimentation of suspended materials increases. These are usually the widest and deepest stretches, and in Idaho they are also indicative of a decrease in the following attributes: channel gradients, channel elevations, and percent of channel composed of gravel (Platts 1979).

An awareness of the transitional changes from the headwaters to the downstream waters, plus the fact that many stream characteristics are similar from one stream to the next, have necessitated a general classification of the various stream reaches (Winger 1981). The term "stream order" has been developed in which each stream section is assigned a number. "Order 1" streams denote the smallest unbranched tributaries of a river, while "Order 2" streams signify the union of two order 1 streams (Strahler 1957 as modified from Horton 1945). "Order 3" streams commence where two second order streams merge, and so on. Stream order is generally indicative of the size and width of stream reaches (Platts 1979; Vannote et al. 1980; Benfield 1981). Stream reaches, then, are aptly characterized as to their morphology and fish populations by the use of stream order (Platts 1979; Mundy and Boschung 1981).

When compared with lakes, the mean depth in rivers may be described as relatively shallow throughout (Table 1). Fishes require a minimal stream depth at all times for cover. The stream shore depth, for example, is critical to fish survival, because it provides a nursery area for first-year cohorts. In addition, depth partially determines stream velocities (Platts et al. 1983), which, in turn, affect ecological diversity in localized areas. Depth variability, so characteristic of rivers, indirectly influences the various biotic components. Deep and shallow areas are usually represented as alternating pools and riffles (Hynes 1970). A 1:1 pool/-riffle ratio is considered desirable when assessing the stream's capability for fish propagation (Platts et al.

1983). Riffles are crucial to the survival of river fishes in that they provide the medium for much of the fishes' aquatic food; in addition, they often serve as spawning and nursery areas and supply cover for subsequent rearing of fry (Platts et al. 1983). On the other hand, pools and streambank undercuts represent fish refugia where cover provides protection for fishes of all ages. Streambank undercuts promote high production rates of young fishes, resulting in high levels of standing stocks (Platts et al. 1983).

Lakes, on the other hand, have relatively high mean depths (Table 1). Shallow areas of lakes generally are found adjacent to shore, where extensive littoral formations may occur. Outer waters, remote from shore, are usually the deepest. The most productive nursery areas are usually found in environmentally diverse situations, especially ecotones (e.g. nearshore littoral, where tributaries enter, offshore shoals, and bays with macrophytes). The littoral areas of lakes are those most analogous to river habitats, and usually contain sand and gravel substrates, low current velocities, reduced light penetration, and well oxygenated spawning and nursery sites (Kitchell et al. 1977). Specifically, the most productive lake areas are to be found at shallow interfaces such as the land-water, air-water, or mud-water zones, and at such depths as are appropriate for photosynthesis.

Seen from above, a river is a long, meandering, ribbon-like water body, unlike the relatively short, ovoid shape of a typical lake. Thus, the breadth/-shoreline length ratio of lakes far surpasses that of rivers. On the other hand, the watershed/surface area ratio of rivers exceeds that of virtually all lakes and accounts, in part, for the inordinately great effect of exogenous processes on rivers (Table 1).

The two types of water bodies converge, however, in the sense that the most ecologically diverse lotic and lentic ecosystems are concomitant with maximum aquatic edge or ecotone. This is likely due to the fact that ecological diversity, in terms of species numbers, is often related to environmental heterogeneity (MacArthur 1972). In rivers, the edge effect furnishes valuable rearing habitat for fishes, and otherwise attracts them to nursery areas (Platts et al. 1983). Since meanders are indicative of increasing aquatic edge and greater depth, and so are physically complex, they create ecological diversity in rivers (Hynes 1970). Analogous to high channel sinuosity is an irregular lake shoreline, which is conducive to ecological diversity in lakes (Moyle and Cech 1982).

Large water bodies, be they rivers or lakes, are usually more complex environmentally than are small water bodies, due to scale factors alone. Darlington (1957) related the size of rivers to the numbers and diversity of fish species; similarly, a greater surface area was indicative of a greater number of species in lakes (Barbour and Brown 1974), as was a longer shoreline (Moyle and Cech 1982). A measure of available ecotone in rivers, similar to the shore development factor for lakes (Hutchinson 1957), would be a useful adjunct to stream survey methodologies.

The lotic environment is typically more turbid than the lentic environment (Table 1). Turbidity levels vary from headwaters to mouth, from river to river, and temporally within any stream (Winger 1981). The muddy-bottomed, downstream areas where the mean particle size of the substrate decreases (Hynes 1970; Smith 1980), are generally the most turbid (Moyle and Cech 1982) except for glacial streams.

Turbidity at high levels may represent an environmental stress (Wallen 1951). Improper land use management, resulting in increased rates of erosion, is often the culprit (Dissmeyer 1976). The consequences of excessive turbidity are as follows: 1) reduced light penetration, and therefore, reduced photosynthesis; 2) altered water chemistry; 3) altered physical habitat; 4) injuries to biota (Cairns 1968; Iwamoto et al. 1978); 5) reduction in standing stocks of benthos; and 6) hindered reaeration (Cordone and Kelly 1961). Turbidity is likely to be more critical in rivers than in lakes (Table 1) because of the vulnerability of the former habitat to rapid changes

in water levels and bank undercutting. The most successful river biota, however, have responded over time by physiological adaptation, or by the development of special structures (e.g. tapetum lucidum, highly sensitive acoustico-lateralis system, barbels or electrical organs) that enhance sight, sound, or the tactile sense (e.g. Nikolsky 1963).

The effects of high levels of turbidity in lakes are essentially similar to those in streams, and normally are not so high as to directly increase mortality rates in fishes (Wallen 1951). Certain fish species (e.g. the sauger, *Stizostedion canadense*, and goldeye, *Hiodon alosoides*) may even require a minimum level of turbidity for optimum levels of behaviour, metabolism or reproduction (Doan 1941; Ali et al. 1977; Ryder 1977).

The consequences of ice formation and movement likely affect the morphology of rivers more severely than is the case with lakes. These effects extend to river biota in the form of physiological traumata. The ice formed on rivers rarely persists for the entire winter in the southern part of the north-temperate zone, unlike lakes where surface ice tends to endure from fall to spring, and persists longer than river ice at the same latitude. The various types of ice formed on rivers, such as "frazil" and "anchor" ice (Hynes 1970), undergo a continuous formation/breakdown process, with the end result being the prevalence of more open-water areas during winter in rivers than in lakes at the same latitude (Table 1).

River beds are susceptible to far greater levels of ice scouring than are most substrates of lakes except for the shallow eulittoral zones of the latter. Many rivers will freeze to the substrate, at least in the nearshore areas, which are most likely to constitute the spawning redds of certain fish species (Platts et al. 1983). Therefore, a greater stress may be placed on the potential spawning and nursery grounds in rivers than in lakes, particularly for fall-spawning fishes which include many of the salmonids.

HYDRODYNAMICS

Lotic ecosystems are characterized by continuously moving, unidirectional flows (except where tidally influenced), which tend to transport matter downstream, and by fluctuations in the

Table 2. A comparison of certain hydrodynamic properties of rivers and lakes found primarily in the north-temperate region.[1]

Attribute	Rivers	Lakes
Flow characteristics	Unidirectional, horizontal	Three-dimensional
Current	Gravitational movement, decreases vertically	Wind-induced, convectional
Flow diversions	Common, habitat implications	Rare
Langmuir vortices	Rare	Frequent
Oil slicks (Taches d'huiles)	Rare	Common
Chemical stratification	Estuarine reaches	Meromictic lakes
Water level fluctuations	Flooding	Minor variations
Flooding effects on biota	Traumatic; reset event	Diminished

[1]Data were derived, in part, from the following sources: Hynes 1970; Ryck 1975; Speaker et al. 1984.

annual water yield (Table 2; Benfield 1981; Speaker et al. 1984). The current and its debris contour the morphology of a river channel; the velocity determines the rate of silt deposition and the substrate type, and influences the biota profoundly (Smith 1980). Characteristics of lotic water columns, and thus velocities, are determined by the following controlling factors: 1) the channel form; 2) the channel gradient; 3) the volume of water in the channel (Platts et al. 1983); 4) the river bank; and 5) substratum type. This tightly-knit complex of interacting variables fluctuates constantly, and acts in concert to determine the varying stream velocities. The velocity of the water column generally increases concomitant to the discharge as the channel widens in a downstream direction, due to the significant depth increases which also occur (Leopold 1953). Nevertheless, width and depth generally increase more rapidly than velocity in a downstream direction (Beaumont 1975).

The current decreases from the surface to the bottom of the river, where a boundary layer (1-3 mm thick) of very slow current exists, forming a thin current refugium for benthic animals (Hynes 1970). Because the effectiveness of the boundary layer is a function of the velocity of water passage over a resistant substrate, this ecological phenomenon is more characteristic of streams than of lakes. In streams, an adaptive biota (e.g. dorso-ventrally depressed body) has been most successful in colonizing riffle areas through the current refugium provided by the boundary layer (e.g. Ambühl 1961).

Structural factors may change stream velocities, divert the direction of flow (Leopold and Langbein 1966), and hence, alter existing stream habitat conditions. Several examples of structures affecting the stream ecosystem throughflow are riffles, falls, rapids, debris, beaver dams, and ice. These, and other flow diversions, are thought to have considerable habitat implications (Hynes 1970). Water retention in streams and rivers, for example, is important in determining food availability for riverine biota (Speaker et al. 1984). Fallen trees may create shoals, dammed sloughs, or on occasion, they may divert flow by completely blocking lowland rivers, thus forming multiple channel rivers, oxbow lakes, and other complex aquatic habitats (Sedell and Froggatt 1984).

The sinuosity of river channels, created by meandering, makes an important contribution to stream habitat. Meandering is both created by, and influences, other hydrodynamic properties of a stream. The dynamics of meandering is a complex subject involving turbulent flow and erosion-deposition processes, important determinators of stream morphology (Leopold and Langbein 1966).

Patterns of flow are also determined by slope and volume of flow, which in turn determine pool/riffle ratios. The more resistant reaches (e.g. riffle areas) are characterized by a steeper slope than are the smooth-flowing areas such as pools (Hynes 1970). Consequently, as the slope decreases and the rate of flow increases, pools and smooth-flowing areas become progressively more prevalent following the turbulent headwater reaches, until the water eventually flows evenly (Neel 1951).

Lake ecosystems are subject to three-dimensional water flows in most cases (Table 2). The currents are largely wind-induced, and these have the potential to affect faunal distribution such as zooplankton and larval fishes, and thus, the distribution of predatory adult fishes (Moyle and Cech 1982). These same currents also affect the distribution of particulate matter and therefore, influence sedimentation rates. However, unidirectional flow patterns may arise in localized areas, as a consequence of thermal bars resulting in coastal currents or currents generated by influent streams (Wetzel 1975). Furthermore, a slight one-way current may exist in lakes between inlets and outlets (Moyle and Cech 1982). Unlike rivers, water movement in lakes is not usually gravitationally induced; however, convectional (gravitational) water movements during spring or fall overturn do occur in dimictic lakes, and remain unique features of them (Table 2). Furthermore, shoals comprised of debris and other lake structures do not form major

obstructions to the flow, as a rule. Debris, however, may be entrained within Langmuir vortices, which are common characteristics of lakes, but which are seldom seen in rivers. "Taches d'huile" or oil slicks, are another feature which are probably unique to lakes (Hutchinson 1957). These are due, usually, to the presence of a phytoplankton-generated oil film on the surface of the water which impedes wind-induced water currents.

A considerable degree of density stratification may occur in the estuarial areas of rivers, where fresh water flows over the incoming salt water (Patrick 1972). Within this context, river estuaries can be likened to a chemically stratified meromictic lake, with the greatest water density, and therefore, the highest salinity concentrations (due to marine intrusions) occurring on the bottom (Table 2).

Odum (1971) suggested that lotic environments are open systems due to flooding, since an exchange of water, sediments, organic matter, and nutrients takes place between stream and watershed when the water impinges upon the land/water interface. In rivers, flooding affects every biotic component (Ryck 1975), whereas the effects in lakes may be substantially less. Floods may scour aquatic vegetation from the stream bed and determine, at least in part, the depositional volumes of silt and organic debris downstream. They may also destroy eggs and young-of-the-year fishes, and suppress benthos, which in turn affects fish production through the food web (Ryck 1975). For example, high flows in Martis Creek, California, caused most species of a fish assemblage to decline in terms of numbers and biomass, whereas, during relatively flood-free seasons, the converse occurred (Moyle and Vondracek 1985). Furthermore, the vulnerability of a particular fish species to flooding increased if their spawning season coincided with periodic floods (Seegrist and Gard 1972; Moyle and Vondracek 1985).

In lakes, water level fluctuations are much less dramatic and potentially less devastating (Table 2). Spring spawners may be affected either favourably or unfavourably by spring flooding. For example, flooding is actually requisite for goldeye reproduction (Sprules 1947).

Ice forms less readily on running water than on standing water, since the mixing action brought about by turbulence will not allow ice formation until river water is uniformly at 0°C (Hynes 1970). Conversely, ice forms more readily on lakes under calm conditions but only the surface waters need reach 0° C for freezing to commence. When rivers do freeze, even those that "freeze to the bed" probably have some free water remaining between and under stones, or in some of the deeper portions (Hynes 1970). We observed that the water depth of several rivers tributary to the north shore of Lake Superior, fell considerably between freeze-up in November, 1985 and mid-January, 1986, judging from the vast air spaces between the ice crust and the water surface, where large sections of ice had collapsed, creating hollows. In all likelihood, the reduced inflow from frozen tributaries and surface runoff is the principal cause of the decreased depth in the main channels in winter.

TEMPERATURE

The composition of the stream community is considerably influenced by the thermal properties of the water. Thermal variation is necessary to influence the seasonal events in the life cycles of fishes, such as spawning and emergence of fry from the spawning redds (Ward 1985). Rivers warm up faster than lakes after the spring break-up, a fact which spring spawners such as yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*) can use to their best advantage (Ward 1985). Generally, lakes take longer to reach their maximum summer temperatures, as spring overturn must precede the ultimate warming of surface waters in north-temperate, dimictic lakes.

Temperatures fluctuate much more rapidly in rivers than in lakes (Table 3), but variations occur within a tight range (Hynes 1970). In fact, both diel and annual thermal periodicity patterns exist for rivers in a seasonal climate (Ward 1985). The diel minima occur in early morning, while the maxima are reached in mid or late afternoon, occur-

Table 3. A comparison of thermal properties of rivers and lakes found primarily in the north-temperate region.[1]

Attribute	Rivers	Lakes
Temperature variation	Fluctuates rapidly	Stable
Density stratification	No	Yes
Temperature maxima	Downstream	Epilimnion
Air temperature effects	Considerable	Diminished
Air-water equilibrium temperature	Water temperature lags behind air temperature except in downstream reaches	Equal to water temperature of epilimnion surface
Temperature cline (summer)	Cold headwaters, warm downstream areas	Cold hypolimnion, warm epilimnion
Groundwater/surface drainage ratio (summer)	High ratio decreases temperature; low ratio increases temperature	Significant only in seepage lakes; effect same as in rivers
Tributary effects on temperature	Considerable	Diminished and localized
Water body size	Large rivers thermally more stable than small streams	Large lakes thermally more stable than small lakes
Shading effects on temperature	Considerable, create thermal stability	Diminished
Floating vegetation effects	Increases temperature	Increases temperature of epilimnion, usually in nearshore littoral
Suspended silt effects	Increases temperature	Increases temperature in epilimnion

[1]Data were derived, in part, from the following sources: McCombie 1959; Hynes 1970; Welcomme 1979; Smith 1980; Ward 1985.

ring later with increasing distance downstream in the northern hemisphere (Schmitz 1954; Yakuwa 1960). Rates of temperature change may be as high as 3°C per hour (Brown 1969), while diurnal temperature variations of up to 6°C may occur due to the absorption of solar radiation or the subsequent release of heat from the water to the atmosphere (Hynes 1970).

Except in great depths of 15 m or more, the main river channel generally remains thermally unstratified due to the mixing action which is achieved by the current (Hynes 1970; Welcomme 1979). Dimictic lakes, however, do possess vertical thermal stratification, which is seasonally dynamic. The epilimnion, the freely circulating surface layer, is the warmest layer and fluctuates along a small temperature gradient (Smith 1980), always at dynamic equilibrium with the air temperature (McCombie 1959). Below this, the metalimnion or thermocline declines rapidly in temperature (at least 1°C for each meter of depth by definition; Welch 1952), but the deepest layer, the hypolimnion, decreases in temperature much more slowly, usually until maximum density is reached at 4°C in north-temperate lakes. Usually, lakes take longer to reach their maximum summer temperatures, as spring overturn must precede the ultimate warming of surface waters in north-temperate, dimictic lakes. In general, then, temperatures of these lakes are more

stable than river temperatures (Table 3), especially in the subsurface layers during the two annual periods of density stratification.

Temperature, an important regulator of metabolism and growth (Fry 1947), is determined to a large degree by climate, stream channel morphology, hydrodynamic properties of the channel, and hydrologic attributes of the watershed (Hallam 1959; Coutant 1975; Ward 1985).

A complex of regional climatic factors act in concert to determine the river's temperature regime. Ward (1985) suggested that air temperature is the most important of these. He noted that air temperature influences groundwater temperature and equilibrium temperature (water temperature at which net heat exchange with the atmosphere is zero). Stream temperatures generally follow, but lag behind the air temperature and therefore, the equilibrium temperature (Ward 1985). Downstream, however, less shading by vegetation exists, and greater surface area is exposed to solar radiation, causing temperatures to increase until a dynamic equilibrium with the air temperature is reached (Hynes 1970).

The source of the water in a river is another noteworthy hydrobiological variable affecting temperature (Ward 1985). If the stream is spring fed, the headwaters and upper reaches are generally cool in summer and warm in winter because the water originates underground (Hynes 1970; Patrick 1972; Ward 1985). The temperatures in the upper reaches of spring-fed rivers remain relatively constant throughout the year, as well as on a daily basis, in comparison to those streams which are fed primarily by surface drainage (Hynes 1970; Patrick 1972; Ward 1985). The relative proportion of groundwater/surface drainage will tend to influence water temperatures. In the spring, snowmelt may either decrease or increase stream temperatures, depending on the type and distance of surface conditions traversed. Similarly, if a river is fed by way of a lake outlet, the ensuing river temperature may reflect, in part, the water temperature of the parent water body.

Tributaries have potentially profound influences on a stream's water temperature (Table 3). They may have higher summer temperatures than the main channel if they are smaller or exposed to more solar radiation (Ward 1985). On the other hand, heavily vegetated stream banks or a greater influx of spring water tend to have a cooling effect in summer.

In lakes, the role of tributaries in determining temperature is less significant and usually localized. The relative volume of inflowing tributary water is often negligible compared to the great volume within a lake, which in itself, greatly enhances the system's temperature buffering capacity. On the same note, springs do not evoke the same temperature effects in drainage lakes as in rivers, due once more to the greater volumetric buffering capacity of lakes.

Morphometry (e.g. width, depth, length) and hydrodynamics are elements of considerable importance in the determination of river temperatures. Small streams, for example, have large thermal fluxes (Brown 1969), while larger rivers exhibit greater thermal stability. Thermal immutability is also relatively greater and in effect for longer time periods during high flow (Ward 1985), making the temperature regime analogous to that of deep, voluminous rivers. Under these circumstances, the water moves at a higher velocity and is, therefore, less subject to being influenced by the ambient temperatures of the air (Ward 1985). As in large lakes, the large volume of water acts as a buffer to external temperature influences.

Stream sections that are shaded by fringing vegetation (i.e. trees, shrubs) or steep, or overhung banks, may be cooler than stream reaches which have large areas exposed to direct sunlight (Welcomme 1979; Smith 1980). These shaded stream areas, which are often headwater reaches, also tend to exhibit a high degree of thermal stability (Welcomme 1979). According to Barton et al. (1985), unshaded streams reach their maximum daily temperatures earlier in the day than shaded streams; however, the two stream types achieve minima at night during comparable time periods.

In lakes, because the ratio of shoreline to surface area is relatively smaller than in rivers, the shading effect of vegetation on the total water body is relatively slight, or even insignificant (Table 3).

Floating vegetation may promote the attainment of very high temperatures in rivers (Welcomme 1979, 1985). Presumably, flood plain rivers and high order reaches, with their associated slow current and lentic characteristics, are most conducive to such accumulations of floating vegetation. If the vegetation is of considerable thickness, evaporation is restricted, sunlight is absorbed, and wind and wave action are reduced; hence, temperature increases may be dramatic. For example, Welcomme (1979) noted temperatures of up to 40°C in an African oxbow lake covered with water ferns (*Salvinia auriculatus*).

Suspended silt also absorbs heat energy, thus increasing temperatures in turbid rivers where large silt loads are being transported (Ellis 1936; Reid 1961). In some areas, however, warmer waters may carry a reduced silt load, flow somewhat faster, and have a thinner boundary layer.

CHEMICAL CHARACTERISTICS

A singular feature of lotic ecosystems is their chemical homogeneity (Table 4), caused by turbulence throughout the water column (Winger 1981). However, the concentrations of various chemicals dissolved in rivers vary greatly according to region, and they reflect such factors as the climate, physiography, geology, and biota (e.g. Hynes 1970; Welcomme 1979). More specifically, factors influencing the surface water chemistry include precipitation, nature of the bedrock, and the dynamics of the evaporation-crystallization process (Gibbs 1970). The "Gaia" hypothesis (Lovelock 1979) invokes biotic factors as controllers of atmospheric conditions

Table 4. A comparison of some key chemical characteristics of water, especially as applied to north-temperate rivers and lakes.[1]

Attribute	Rivers	Lakes
Vertical chemical profile	Homogeneous	Stratified
Diel periodicity for various chemicals	Yes	Yes, at interfaces
Dissolved gases in dynamic equilibrium with atmospheric gases	Yes	No
Oxygen content	Usually high	Variable
Oxygen uptake ability at water surface	High	Variable
Diurnal variation of dissolved O_2	Yes - dependent upon photosynthesis, respiration rates, and decomposition	Not significant
Phosphorous	Variable spatially (headwaters to mouth)	Variable temporally (high in spring and at turnovers)
Total dissolved solids	Increase downstream	Temporal cycle
Turbidity	High - varies among rivers and spatially	Low - varies among lakes and temporally

[1]Data were derived, in part, from the following sources: Hynes 1970; Smith 1980; Winger 1981.

through feedback, which provides desirable biospheric conditions. As an ultimate consequence, chemical stoichiometry in rivers may be under the regulation of the biosphere through biogeochemical homeostasis (e.g. Holling 1985).

Müller (1974) proposed that the diel cycle, of alternating light and dark periods, induced variations in both physical and chemical factors. This cycle, he maintained, "determines the development and locomotory processes of uni-cellular algae", thereby, not only influencing the development and behaviour of invertebrates and fishes, but also affecting dissolved oxygen, carbon dioxide saturation, as well as pH and silicon levels via algal photosynthesis (Müller 1974; Winger 1981).

Winger (1981) categorized stream chemicals into five classes of compounds: 1) dissolved inorganic ions and compounds; 2) particulate inorganic compounds; 3) dissolved organic compounds; 4) particulate organic material; and 5) dissolved gases. The dissolved gases in lotic ecosystems, such as oxygen, nitrogen and carbon dioxide, are generally in dynamic equilibrium with the atmosphere (Hynes 1970).

Dissolved oxygen levels in rivers are rarely inadequate for the respiration of biota and putrefaction processes (Winger 1981); in fact, in small, turbulent streams, the oxygen content may transcend the saturation point during certain seasons (Hynes 1970; Smith 1980). The two major sources of dissolved oxygen in streams are the water-air interface zone and photosynthesizing plants. In the first instance, turbulent waters have greater surface area contact with the atmosphere, thus, oxygen uptake is facilitated (Smith 1980). Hynes (1970) noted that the amount of air uptake varies approximately with the velocity, and that air can comprise up to 60% of the water volume.

Variations in the dissolved oxygen content of rivers do occur, both diurnally and seasonally. The diurnal variations are largely dependent upon the rates of photosynthesis and respiration of the stream biota (Hynes 1970). Seasonal variations in oxygen may also take place due to: 1) leaf inputs in the fall, which increase oxygen demand; 2) seasonal photosynthesis peaks and declines; 3) winter ice-cover on rivers, which serves to decrease oxygen levels; and 4) high discharge situations which tend to reduce the oxygen content (Hynes 1970). Dissolved oxygen and carbon dioxide are generally inversely related, because of photosynthetic and respiratory rates of stream organisms (Hynes 1970) as well as the decomposition of organic matter (Winger 1981).

It is well known that lake oxygen levels, which are usually highest in the surface areas, decrease with depth (Smith 1980). Dissolved oxygen in lakes, while generally lower than in rivers (Smith 1980), also originates from both the atmosphere and from photosynthetic activity of plants. Under certain circumstances, the latter activity may result in supersaturation levels or alternatively, result in a net oxygen deficit (e.g. Hutchinson 1957). Oxygen depletion in lakes, as in rivers, may be severe under the ice and may result in heavy losses of fish in winter.

Total dissolved solids (TDS) tend to increase in the downstream reaches of streams (Winger 1981). The major cations contributing to TDS in rivers, in descending order of concentration, are generally calcium, magnesium, sodium and potassium (Funk 1970). However, the prevailing chemicals may differ according to the local geology and climate. High concentrations of calcium, sulfates, and carbonates are present in the rivers of humid, temperate regions. Arid or semiarid areas are typically high in sodium, sulfates and chlorides (Funk 1970; Winger 1981). Calcareous rivers are generally the most productive (Hynes 1970), which is true also of calcareous lakes. Silicon is another element essential to the survival of river biota. It is an especially dominant component in granite/sandstone regions where the TDS in streams are typically low (Funk 1970). The levels may fluctuate between 2 and 9 mg L^{-1}, since SiO_2 is depleted as diatoms replace the lost halves of their shells subsequent to cell division (Müller 1974).

Phosphorous is the element which is

most often a limiting factor in primary production of freshwater ecosystems (Hutchinson 1957; Schindler 1977). Therefore, its concentration, spatial distribution and temporal regime are important, and even critical to the metabolism, and hence, survival of organisms in both rivers and lakes. The major allochthonous sources of phosphorous in both streams and lakes are rainfall and the land surface of the immediate watershed (Hutchinson 1957; Hynes 1970). However, in lakes, a larger proportion of available phosphorous may be of autochthonous derivation than in rivers, the latter being more strongly influenced by the abiotic environment (Sanders 1972). While phosphorous concentrations may vary in time and space in both rivers and lakes (Table 4), the largest variations for rivers would seem to be spatially organized, from headwaters to mouth, while for lakes, temporal variability is usually greatest. Both rivers and lakes in the north-temperate zone usually reach annual high phosphorus concentrations during the spring runoff period (Table 4; Dillon and Rigler 1975).

TROPHODYNAMICS

Rivers have been described as continua, or gradients (Cushing et al. 1983), in which "ecosystem level processes in downstream areas are linked to those in upstream areas" (Minshall et al. 1985). This implies a dynamic, longitudinally-linked system, in which a conspicuous transition occurs from headwaters to downstream reaches. Many of the headwater regions are typically forested; hence, erosion is minimal and the water is clear (Patrick 1972). As a result, photosynthesis may occur across the width of the stream (Patrick 1972); presumably, this is true only in wide, unshaded stretches of headwater streams. Alternatively, if the headwaters are narrow, the extensive shading of riparian vegetation may not only limit photosynthesis considerably, but may also supply large amounts of allochthonous matter in the form of leaves (Vannote et al. 1980). Certainly, al-

Table 5. A comparison of some trophodynamic processes, especially as applied to north-temperate rivers and lakes.

Attribute	Rivers	Lakes
Primary energy and nutrient sources	Allochthonous	Autochthonous
Secondary energy and nutrient sources	Autochthonous, meteorological, and geological inputs, tributaries, seepage	Allochthonous, meteorological, and geological inputs
Allochthonous/autochthonous ratio	Decreases in downstream direction	Decreases with increasing age in eutrophic systems
Rate of nutrient influx	Governed by terrestrial vegetation, flooding	Determined by internal cycling rates
Speed of nutrient transit	Rapid, determined by gradient/current	Slow, determined by wind/waves, overturn
Nutrient retention	Low	High
Course of nutrients	Downstream progression; constant renewal of dissolved nutrients; nutrient spiralling	Nutrients primarily recycled in place

Data were derived, in part, from the following sources: Hynes 1975; Webster 1975; Welcomme 1979; Moss 1980; Smith 1980; Minshall et al. 1985.

lochthonous detrital inputs have been universally touted as being the primary energy source in lotic ecosystems (Table 5; Hynes 1963, 1975; Cummins 1975; Cummins and Klug 1979; Welcomme 1979; Moss 1980). Organic input enters the stream in three major size categories: coarse particulate organic matter (CPOM >1 mm diameter; Vannote et al. 1980), fine particulate organic matter (FPOM 0.5 um - 1 mm), and dissolved organic material (DOM <0.5 um; Smith 1980; Benfield 1981). The organic carbon supply in rivers is furnished primarily by allochthonous organic material (Moss 1980); however, it is usually complemented by significant amounts of aquatic plant production, both spatially and seasonally (Minshall et al. 1985).

The importance of the terrestrial vegetation and adjacent land areas in influencing the stream trophodynamics is currently well recognized (e.g. Cummins et al. 1984; Minshall et al. 1985). The stream and its valley, or surrounding watershed, are strongly interrelated, as indicated by Hynes (1975). He suggested that the slope of the valley, the depth and porosity of the soil, and the patterns of precipitation are powerful influences on the rate of flow and the DOM content of streams. Moreover, he felt that the type and density of the terrestrial vegetation, as well as its inherent chemical, biological and physical dynamics (Cummins et al. 1984) were critical in the processing rate. More specifically, the terrestrial vegetation which acts as a storage facility for various mineral elements, determines the rates at which various ions, such as calcium, magnesium, potassium and nitrogen are delivered to the stream.

While a lake may be considered to be a self-contained ecosystem, bioenergetically speaking (e.g. Forbes 1887; Thienemann 1953), it is, nevertheless, influenced by external forces. Allochthonous detritus, meteorological inputs such as wind-borne particulate matter, substances dissolved in precipitation, atmospheric gases, and geological inputs such as nutrients dissolved in groundwater, inflowing streams, or runoff are all important elements in lakes (Schindler and Nighswander 1970; Smith 1980). Moreover, nutrient and energy sources may be divided between allochthonous and autochthonous sources, depending on the successional stage. In consideration of a cline of lakes ranging from high nutrient loading rates or eutrophic, to low rates (oligotrophic), the former must rely relatively heavily on allochthonous nutrient inputs from its watershed, while the latter are most dependent upon internally recycled, autochthonous nutrients. As a rule, the allochthonous component of energy and nutrient input via leaf litter is relatively low in lakes. This is due, in part, to the low rate of inflow in lakes, and the reduced effect of the riparian zone in the offshore waters. However, the fact that autochthonous sources play a more important role in lakes (Table 5), is due to the relatively large water volumes at the lake's surface that are conducive to photosynthesis and hence, primary production. On the other hand, autochthonous sources in rivers generally supply a smaller amount of energy and nutrients due, in part, to high turbidity levels, a near absence of phytoplankton, and relatively few macrophytes, although the effect increases downstream (e.g. Vannote et al. 1980).

Hynes (1975) described riverine ecosystems as being largely heterotrophic, in the sense that they continually derive energy from upstream sources. However, strongly autotrophic regions often exist as well, especially in the midreaches, according to Vannote et al. (1980). Autotrophic components may, therefore, make considerable contributions to the primary production in a river (Hynes 1963; McIntire 1975), especially large rivers and flood plain systems (Sedell and Richey 1988). Therein, a general pattern emerges, which is applicable to many lotic communities: the headwaters, if shaded, are primarily heterotrophic; in the midreaches, where the effects of the riparian vegetation are reduced, autotrophy increases; and further downstream in more turbid waters the river reverts back to heterotrophy.

Analogous to the heterotrophic-autotrophic-heterotrophic transition as rivers are traversed from headwaters to mouth (Vannote et al. 1980), is the

change in lakes from autotrophy in the euphotic portion of the limnetic zone to heterotrophy in the dark profundal zone (Moss 1980).

Not only does the ratio of allochthonous/autochthonous inputs decrease in a downstream direction in most rivers, but the relative importance of the various invertebrate functional groups (e.g. shredders, collectors) tends to shift concomitantly. These represent a crucial link between the abundant microorganisms and fishes, and have been assigned to categories that are descriptive of their food acquisition habits by Cummins et al. (1984). Invertebrate "shredders", for example, exist largely in upland streams or headwaters (Moss 1980; Benfield 1981), and are the first to attack litter (Hynes 1975), utilizing CPOM such as leaves and twigs (Vannote et al. 1980; Cummins et al. 1984). The fact that shredders glean the microbial biomass associated with leaf litter is more than coincidental; rather, these invertebrates seem to possess an inherent dependence upon these tiny organisms (Cummins 1974; Cummins 1975; Jones 1975; Cummins and Spengler 1978; Vannote et al. 1980). Of the total material ingested by invertebrates, approximately 60% contributes to the FPOM in the form of fecal matter (Smith 1980), which in turn, is consumed by other organisms (Hynes 1975). In the midstream reaches, for example, "collectors", such as Simulidae (Smith 1980), filter FPOM from the water column or from the sediments, and they, like shredders, depend for nourishment upon the bacteria and fungi associated with the FPOM (Vannote et al. 1980). Another type of midstream primary consumer, the "scrapers" or "grazers" (e.g. snails, freshwater limpets, water pennies, caddisflies, and some mayflies) feed on the algal coating of stones and rubble (Moss 1980; Benfield 1981). They usually exhibit morphological adaptations appropriate to their particular functional role. The insect larvae may, for example, possess stiff bristles or mouth parts, while snails possess radula, or toothed organs (Moss 1980). In the downstream areas, where the FPOM is present in the greatest volume, the emphasis shifts to collectors (Benfield 1981).

Secondary sources of biotic energy in rivers generally include subsurface seepage (Welcomme 1979), precipitation and tributary inputs. As Hynes (1975) noted, overland flow is not necessarily synonymous with runoff, but rather, it is often due to the displacement of old ground water by new rainfall seeping into the ground. He suggested that the role of vegetation is important, as transpiration dries up the soil in the vicinity of a river during the summer or dry season, which, in turn, provides space for new winter or wet season precipitation. In some areas, where rocks are poor in nutrients, and the soils are leached (as in the case of tropical laterites), precipitation may indeed account for the primary input of stream nutrients (Welcomme 1979).

Tributaries may also enhance the levels of nutrients in the main stem if the concentrations of nutrients and/or food items in the tributaries exceed those of the main channel (Ryder 1964; Minshall et al. 1985). Alternatively, a tributary may serve to dilute nutrient concentrations or provide a new avenue for CPOM influx. Hence, the characteristics of a particular stream section, downstream from the influent of the tributary, may be reminiscent of the upstream reaches.

The rate of nutrient influx also depends largely upon the degree of flooding and the numerous effects of the terrestrial zone (Sanders 1972; Hynes 1975). Local flooding of banks may occur due to the natural obstructions present in the water column, thus providing an additional source of nutrients (Sanders 1972). Flooding results, therefore, in large inputs of FPOM and DOM when water enters the stream following flooding (Hynes 1975).

The unidirectional flow, so characteristic of rivers, results in a rapid transport of nutrients in a downstream direction (Table 5), especially where nutrient retention mechanisms are limited. Both producers and consumers must be adept at rapid nutrient uptake, especially the sessile biota which cannot pursue their food items. The river biota essentially depend upon the steady nutrient replacement via allochthonous debris and nutrient or detritus

displacement from upstream. The latter occurs largely via runoff and groundwater inflows (Patrick 1969).

Nutrient retention mechanisms within rivers allow processing and nutrient distribution in localized stream sections. Thus impeded, food is rendered available to riverine biota (Speaker et al. 1984). High gradient streams, typified by steep slopes, often have a high leaf litter input as well as a high rate of retention (Sanders 1972). Important retentive features of rivers include debris dams (Triska 1984), macrophytes (Benfield 1981), and riparian zone vegetation (Cummins et al. 1984), in the form of roots and overhanging, partially submerged branches, as well as the large tree trunks from which they are derived. Logs or fallen trees are important retention mechanisms which sometimes cause flooding of the riparian zone (Minshall et al. 1985). Subsequently, trees may drown and eventually represent a further addition of allochthonous material to the river.

Some nutrient cycling in place occurs in rivers where materials are retained by obstructions (such as those listed above); hence, the loss of some FPOM to downstream reaches is prevented (Benfield 1981). Webster (1975) termed the cyclic downstream movement of nutrients in rivers "spiralling", and he noted that the process tends to maximize utilization of available FPOM. The tightness and magnitude of the spirals is indicative of a stream's ability to process nutrients. Further, spiralling is a mechanism whereby stream ecosystems may withstand and recover from disturbances (Minshall et al. 1985). Invertebrate collectors may be instrumental in the retention process when they consume FPOM (Wallace et al. 1977). In the highly retentive low orders (1-3), spirals tend to be tight, and conversely, they are separated by long distances in downstream locations (Minshall et al. 1985). Spiralling distance appears to be affected primarily by the current velocity and the frequency of retention devices, whereas biological processes are of less significance (Minshall et al. 1985).

Lentic ecosystems may be viewed as nutrient reservoirs, where internal nutrient cycling is an on-going process (Table 5). Unlike rivers, with their characteristic, unidirectional, and rapid nutrient transport, demanding constant replacement from upstream, lakes are more self-sufficient in terms of nutrients. Lentic nutrients are recycled as a rule, and are subject to slow, current-induced movements through the water column or by migrations of the biota.

The rate of decay in rivers, or the microbial activity, depends upon the type of litter, ionic nitrogen availability, and probably the presence of phosphate or other chemicals (Hynes 1975). It would seem reasonable to assume that the decomposition rate is further influenced by the abundance and types of invertebrate consumers present in a certain stretch of river. Indeed, the reduction of lotic insect fauna may decrease shredding and other breakdown activity, subsequent utilization, and downstream transport of organic matter (Wallace et al. 1977). Warm temperatures may also enhance the rate of decay by increasing microbial activity; hence the warmwater, high order streams may exhibit more rapid rates of decay. In light of the above, Wallace et al. (1977) consider the consumers to be the governing forces in both the transfer of energy and the recycling of nutrients.

ECOLOGICAL PHENOMENA

ABIOTIC CONTROLS

The contribution to stream environment by several morphological properties such as gradient, width, depth, substrate type, riparian vegetation, and other related factors, is enormous, and confounded by a myriad of interdependencies that vary from one stream to another (e.g. Minckley 1963; Hocutt and Stauffer 1975; Winger 1981). This pervasive morphological influence is further complicated by the direct and significant effect it has on the abundance and distribution of stream biota, through the hydrodynamic properties of the stream (e.g. velocity, discharge), which are also determined and controlled, to a large extent, by stream morphology.

Accordingly, morphology, hydrodynamics and temperature are inextricably interrelated, and together they form the principal components of the abiotic milieu.

While morphology, hydrodynamics and water temperature, acting in concert, are the three major factors determining species distributions and abundances, a single factor, in some instances, may exceed the combined effect of all others in determining whether a fish or invertebrate may exist in a particular stream reach, and in what numbers. Ergo, a stream gradient approaching the vertical, may preclude the existence of virtually all inhabitants, except for those torrentially-adapted forms such as the hillstream loaches (Homalopteridae; Nelson 1976). Consequently, a stream possessing such an extremely steep gradient may be almost completely depauperate of fauna, harbouring only one or two torrential species, despite an otherwise favorable environment. Hence, gradient, *per se*, appears to be a dominant, overriding force in influencing biota, and does so primarily through the agency of stream velocity.

Chemical effects on the stream environment, in general, are not paramount, unless one or more chemicals are so astoichiometrically imbalanced (Stumm and Morgan 1970) as to affect metabolism or growth of invertebrates or fishes. This happens but rarely in north-temperate streams, except for the often severe effects ascribed to anthropogenic inputs. For biotic considerations, chemical assessments of streams may, in effect, be nutrient assessments, particularly in the case of phosphorus. Chemical composition of stream water, therefore, may be more important as a determinant of their productivity rather than as a limitation to biotic distribution.

Lakes are also provided with an ambience suitable for their biota through their principal morphological properties, which together with climate, determine the seasonal hydrodynamics regime (e.g. Rawson 1952, 1960). Lake depth, area, and volume are closely correlated (Hayes 1957; Kerekes 1976), and in north-temperate dimictic lakes, are critical to the duration and extent of spring and fall overturns as well as wave dynamics, the two predominant features of hydraulic activity in lakes. These influence the chemical composition of lake water which is critical to their productivity, particularly the phosphorus content. As most of the primary productivity in lakes is dependent upon photosynthesis rather than on inputs of allochthonous detritus, nutrient composition of lakes becomes an important consideration, not only from a production standpoint, but also for the determination of species composition (e.g. Marshall and Ryan 1987).

BIOTIC ACCOMMODATION

Huet (1959) has categorized the running waters of Western Europe according to stream gradient or slope and the cross-section of a stream and its valley. In his classification scheme, he identified characteristic properties for each of four "fish zones". Hence, low order reaches or headwaters were classified as "trout zones", typified by steep gradients, rapid flow and cold waters. Downstream from the trout zone was the "grayling zone", a zone of rapidly flowing water, and generally larger channel. The gradient there was less than in the trout zone, and riffles were separated by pools. In another zone downstream from the grayling zone, the "barbel zone", quiet water was the most prevalent, interspersed with rapids. The last zone was a "bream zone", situated in the high stream orders, and therefore, in the lower stretches of large rivers. It had but a slight current, high summer water temperatures, and low dissolved oxygen.

Huet's (1959) stream classification noted changes in each zone, usually constituting a cline from headwaters to mouth. Hence, gradient and dissolved oxygen generally decreased, while stream width and depth, discharge, temperature and turbidity increased, each factor having some influence in determining the species composition and abundance in any particular zone. While stream classification by zone or reach may be of little ecological value because streams are best viewed as gradients or continua (Cushing et al. 1983), we believe that there is significant practical merit to

the former approach viewed from within the latter context. Accordingly, we propose that a zonal, or reach approach may be logistically valuable from a sampling perspective, to address a complex problem in a pragmatic and tractable manner. In this regard we concur with the conclusions of Macan (1961) in Hawkes (1975), who observed that any classification framework for stream ecology should be used--"to stimulate thought and further research, rather than [as] a cage to confine it." Zonal research should be planned, however, within the conceptual understanding of the River Continuum Concept (Vannote et al. 1980), and subsequent analyses effected accordingly.

Other stream classification systems have been proposed, some of greater complexity than Huet's (1959) relatively simple schema (e.g. Margalef 1960; Platts 1979). Most of these classifications are of considerable heuristic value in any progression towards an increased understanding of stream ecosystems.

In lentic waters, vertical density zonation effectively stratifies temperature, oxygen, phosphorus and other nutrients and chemicals. The different zones of the water column are inhabited by different fish assemblages, particularly in oligotrophic lakes. For example, the warm upper, epilimnetic zone, in summer, is typically inhabited by components of a percid community, including the walleye, yellow perch, northern pike (*Esox lucius*), and white sucker (*Catostomus commersoni*), while the lower, cold hypolimnetic zone contains salmonid community members including the lake trout (*Salvelinus namaycush*), burbot (*Lota lota*) and several coregonines (Ryder and Kerr 1988). Hence, separation of two different fish assemblages, living sympatrically within a dimictic lake, depends on depth and temperature primarily, while gradient and temperature would seem to be more important in streams. Segregation of fish assemblages in different lakes (allopatric), is dependent primarily on a lake's trophic level, particularly when measured in terms of temperature and phosphorus (Ryder and Kerr 1988; Ryan and Marshall in prep.).

PRODUCTION, DIVERSITY AND DRIFT

Protoplasm elaboration by stream communities depends upon energetic inputs in the form of allochthonous organic matter in the low orders upstream (Cummins 1974); increasing autotrophic production by algal periphyton and phytoplankton in a downstream direction, climaxing in the middle orders; and heterotrophic production in the high numbered orders towards the stream mouth (e.g. Vannote et al. 1980). Within orders, productivity varies according to substrate type such as sand and bedrock, which are the least productive (Smith 1980). A gravel-rubble bottom tends to be the most conducive to high levels of production, as it not only serves as shelter for invertebrates, but also provides a larger, more stable surface for the attachment of aufwuchs communities, and is eminently suited as a clean and well-oxygenated spawning substrate for fishes.

As a stream is traversed from headwaters to mouth, many factors combine to augment production rates, including higher water temperatures, increased photosynthesis, greater drift volume, higher nutrient levels, greater area of incident solar radiation, more FPOM, as well as other factors (e.g. Hynes 1970; Vannote et al. 1980; Minshall et al. 1985). Factors detrimental to production going downstream may include increased inorganic turbidity and decreased oxygen levels. Production/biomass ratio is lowest at the headwaters, gradually increasing downstream, with greatest production levels occurring at the mouth.

In lakes, the highest production levels occur in eutrophic waters, and lowest in oligotrophic waters (Hutchinson 1957; Wetzel 1975). Primary production in lakes is mainly dependent on photosynthesis by pelagic algae, periphyton and littoral macrophytes. Essential to the production processes in lakes is the biofeedback of autochthonous nutrients, in contrast to the normally unidirectional flow of nutrients in rivers. Rivers, therefore, tend to be more open-ended than lakes,

and depart further from the definition of a microcosmic system sometimes applied to lakes (e.g. Forbes 1887).

Taxa diversity in running waters is both a spatially variable attribute (generally highest in the middle orders; Vannote et al. 1980), and a temporal variable for any given reach. Hence, certain taxa are sequentially replaced by other taxa at any given stream location, dependent on the mean levels of specific environmental variables. This temporal diversity is seasonally determined, and as one taxon is drawn further and further from its seasonal optimum, another functionally similar species is drawn closer, and physically and functionally replaces the first organism (Cummins 1974; Minshall et al. 1985).

Biotic diversity in lakes tends to be more stable over time, and is more likely to be exemplified temporally, in terms of cohort diversity, rather than species succession. Greatest species diversity in the north-temperate zone occurs in mesotrophic lakes where species may be drawn from as many as three community types (Ryder and Kerr 1978).

Organic drift (Waters 1969; Muller 1974), comprised mostly of suspended particulate matter and invertebrates, which are propelled by the current, is a stream phenomenon not known in lakes. It presents a more or less continuous stream of food organisms to both fishes and invertebrates without the necessity for energetic losses experienced by lake fauna in search of their prey. This passive mode of feeding in rivers, however, necessitates the maintenance of position in the water column. In certain instances, fishes feeding on drift may assume levels approximating fishes feeding *ad libitum* in aquaria, which likely explains why running waters are typically much more productive than their standing-water counterparts at the same latitude (Odum 1956; Blum 1972).

RESET EVENTS

Periodic, natural events in lotic environments, such as seasonal floods or drought, may be traumatic to indigenous stream biota. These externally induced events may also be episodic in frequency and essentially unpredictable in terms of their temporal sequencing. Both types of destabilizing events, whether of periodic or episodic occurrence, are termed reset mechanisms, or simply, resets (Cummins et al. 1984; Minshall et al. 1985). Resets are generally associated with the lotic environment, but are not exclusive to them. Because streams are much more vulnerable to exogenous effects than are lakes in general, stream resets tend to be more dramatic. Nonetheless, the trauma induced is usually short-lived, and resets are now believed to be essential to the maintenance of normal community structure in streams (Cummins 1977; Cummins and Spengler 1978) through the relegation back to pioneer community status (Margalef 1960; Cummins et al. 1984). Stream organisms are well adapted to both regular and irregular resets, and recuperate quickly through the use of one or more adaptive mechanisms (Minshall et al. 1985).

Stream resets are often introduced through flooding and subsequent scouring of the stream bed and banks (Douglas 1958; Cummins and Spengler 1978). In unprotected substrates the mean age of some invertebrate populations remains relatively young due to repetition of this process, while in protected environments, invertebrate populations are skewed towards old individuals (Minshall et al. 1985). In the north-temperate climatic zone, floods during the spring spate may be particularly damaging, not only to the stream bed and banks, but also to the riparian vegetation and stream fauna. This effect is induced following a buildup of an ice dam, which may raise the water level markedly. The combined effects of warming weather and water accumulation eventually cause the ice-dam to break, and a massive volume of water and ice flush suddenly downstream, both in the main channel and along the flood plain on either side of the main stem. This phenomenon on large rivers has reached extreme levels known to uproot trees and wipe out human dwellings. In one extreme instance on the Winisk River in Northern Ontario, ice dams at the river mouth caused the river to rise 16 m above its normal level. The subsequent flood eradicated a village built on the

flood plain of the river, and floated 40 houses and other human structures downstream, resulting in two deaths (Thunder Bay Chronicle Journal, Oct. 4, 1986).

Reset events on lakes are generally less damaging to the environment and, therefore, less traumatic to the biotic communities. Spring and fall overturn may be considered "low key" reset events of only minor significance in terms of community alteration, although ecologically important for other reasons. Their main effects are to redistribute the community components according to their preferred temperatures, and to recycle nutrients.

Autumnal, equinoctial storms, accompanied by high winds and rain, may constitute a more severe and damaging reset event on large lakes. Damage would be greatest at the nearshore littoral zone, and fauna and flora there would be most affected. On the other hand, some species such as lake trout seem well adapted to such incidents. Successful reproduction of lake trout, in general, obliges them to spawn on clean, windswept shoals in the fall (Martin 1957), and periodic, equinoctial storms may be instrumental in providing these ideal conditions.

HYPORHEIC ZONE

The hyporheic zone (Orghidan 1959), that subterranean portion of a river that lies between the surficial substrate deposits of the rhithron and the phreatic (groundwater) zone, has been an enigmatic and much neglected stream biotope (Hynes 1970; Pennak and Ward 1986). It has often been observed that rivers are in "intimate contact" with groundwater aquifers (Ward and Stanford 1988) and that their interactive nature exerts a strong influence on habitat conditions. The hyporheic zone has been recorded as deep as 4.2 m under the substrate of the main river channel (Stanford and Gaufin 1974). In Europe, it has been observed to extend laterally under river banks for at least 3 m (Orghidan 1959), and in North America it may exceed this, extending as much as 50 m (Stanford and Gaufin 1974).

Within our present context, the hyporheic zone may be viewed as a unique refugium of streams, which mitigates or biologically buffers the traumata induced by reset events. There, shelter is provided for many invertebrate organisms (e.g. Pugsley and Hynes 1986), which may permit them to escape physiological stress from extremes of temperature and current, droughts and floods, or predation (Orghidan 1959; Hynes 1970). The hyporheic zone, therefore, may be a critical environmental feature of a river by providing a constant reservoir of organisms for recolonization of river substrate following a reset event.

Within the substrata of most lakes, conditions required for the establishment of an inhabitable hyporheic zone of any substantial depth do not exist. Eutrophic lakes, in particular, have deep layers of organic sediments overlying their substrates, which may create inhospitable living conditions for aerobic organisms, due to the by-products of putrefaction (e.g. Hutchinson 1957; Mortimer 1971). In these instances, only a few centimetres of substrate immediately below the mud-water interface zone may be inhabitable by facultative anaerobes. Studies in Swedish Lake Malaren, a mesotrophic lake with dissolved oxygen in the bottom waters generally in abundant supply, showed invertebrate organisms no deeper than 20 cm within the bottom muds (Milbrink 1969). Only the wind-swept and wave-washed littoral of oligotrophic lakes offer anything akin to a stream environment for benthic organisms (Borner 1917 in Brinkhurst 1974; Kitchell et al. 1977). There, the large particle size of the substrate materials and the continual removal of fine organic sediments, through wave action, allow for deeper penetration of the bottom by aerobic organisms. Nonetheless, a true hyporheic zone in the sense of Orghidan (1959) is only approached but not attained in lakes. As most reset events for lakes are not as traumatic as those for streams, a deep substrate recolonization refugium for lakes would not likely be an ecological necessity.

COMMUNITY DYNAMICS

The ways in which aquatic communities achieve dynamic equilibrium differs between streams and lakes. Fish assemblages, for example, are said to be stochastic in streams, because of periodic extinctions of species due to reset events, followed by recolonization from riverine refugia (Grossman et al. 1982). This stochastic school of thought holds that dynamic equilibrium is not possible in stream fish assemblages as it is in lake fish communities, which are deterministic systems because the physico-chemical environment is usually stable enough for the achievement of steady-state. It follows that stream assemblages of fishes are highly variable in their composition and therefore, unpredictable. In general, the well-being of stream fishes is determined more by environmental variability than by biotic interactions.

Recently, it has been proposed that stream assemblages have aspects of both stochasticity and determinism, the latter resulting in a higher level of predictability (Minshall et al. 1985; Schlosser 1985). The deterministic aspects of lotic ecosystems are exemplified by the apparent resiliency of stream biota to reset events.

With respect to lakes, communities tend to be even more deterministic and therefore, more predictable. This is all relative, of course, and applies principally to integrated, co-evolved assemblages of species, sometimes called harmonic communities (Ryder and Kerr 1978). Harmonic communities in lakes are subject to organizational distortion both seasonally and from year to year, but unless subjected to a cataclysmic event, tend to retain their fundamental identity. Astatic assemblages of fishes or other organisms (e.g. Ryder and Kerr 1988) are usually formed through human intervention, and have a tendency towards greater stochasticity and less predictability.

BIOTA

FLORA

Stream flora are comprised for the most part of periphyton and macrophytes, phytoplankton being relatively unimportant except for the slowest flowing reaches (Table 6). And while detritus is paramount as an energy source in streams, particularly in the low order reaches, primary producers become increasingly important downstream, reaching their greatest proportional contribution to production in the intermediate stream orders (Vannote et al. 1980).

The ratio of autotrophy to heterotrophy generally increases from insignificant levels in the heavily shaded, low order streams to a maximum in the wide, intermediate stretches. The microproducers (e.g. diatoms, blue-green algae, green algae, water mosses) and macroproducers, or vascular plants, are the primary photosynthesizers in the middle reaches (Cummins 1974; Sumner and Fisher 1979). The intermediate stream sections, as well as the high orders, are noted for the presence of phytoplankton, especially in large rivers (Cushing 1966), except for those areas where velocity, turbidity, temperature, and nutrient factors may be limiting (Hynes 1970; Benfield 1981). While primary productivity in some stream reaches may be limited by the amount of shading by the riparian forest, as well as the water's chemical composition, the shading of lentic waters is relatively less extensive, as are turbidity levels, thus allowing enhanced pelagic algal growth. In lakes, where water levels are more stable, phytoplankton tends to be discontinuously distributed, but essentially ubiquitous in the euphotic zone (e.g. Hutchinson 1961).

Certain features are compensatory, however, for the generally lower light regime in rivers. The transport and re-

Table 6. A comparison of selected adaptive attributes of stream and lake flora, especially as applied to the north-temperate zone.[1]

Attribute	Rivers	Lakes
Effects of riparian vegetation shading	Extensive	Insignificant
Major contributors to primary production	Microproducers, macroproducers, periphyton, phytoplankton in large rivers	Phytoplankton, macroproducers
Production-to-biomass ratio	Increases downstream	Increases near shore
Primary productivity	Relatively high	Relatively low
Respiratory rates	High	Low
Mineral uptake rates	Rapid	Slow
Floral distribution	Reliant upon nutrients, current	Dependent on depth, substrate
Phytoplankton abundance	Low; greatest in intermediate or large orders; limited by turbidity, turbulence	High
Algal adaptations	Numerous, attached	Primarily pelagic
Bryophytes/lichens	Prevalent; fast-flowing areas, shade tolerant, some limited by hard water	Scarce
Macrophyte adaptations	Few restricted to running waters	Many
Current-induced size reduction of macrophytes	Present	Absent
Floating plants	Limited to slow-flowing reaches; prevalent in tropical rivers	Restricted to sheltered bays

[1]Data were derived, in part, from the following sources: Odum 1956; Nelson and Scott 1962; Whitford and Schumacher 1964; Cushing 1966; Hynes 1970; Blum 1972; Patrick 1972; Cummins 1974; Welcomme 1979; Benfield 1981; Cummins et al. 1984.

moval action of the current greatly enhances processes such as photosynthesis; thus, lotic primary production is somewhere on the order of 6-30 times higher than observed for primary production in lentic environments (Table 6; Odum 1956; Nelson and Scott 1962; Hynes 1963; Blum 1972). Production is heightened as the current disseminates reproductive bodies and rids local areas of excretions and excreta, while cleaning and releasing the more firmly attached species (Blum 1972; Benfield 1981). Moreover, lotic species may exhibit higher respiratory rates and more efficient mineral uptake than the related lacustrine species (Whitford and Schumacher 1961). Other adaptations by stream vegetation, aside from macrophytes (Hynes 1970), enhance nutrient uptake; for example, a large surface-to-volume ratio and a body form which allows maximum contact with the moving water, have evolved in a lotic environment (Blum 1972).

Upstream plants are able to maintain a competitive advantage over downstream plants, the former being in a more

logistically favorable position from which to garner the dissolved nutrients, which are constantly renewed through runoff or ground water (Blum 1972). In some systems, however, it would seem likely that these effects of relative stream position may be compensated for, or overridden by, the rate of nutrient influx via runoff, subsurface seepage and tributaries. The sporadic, unpredictable nutrient influxes may be responsible for the low "equability" (or evenness of distribution of some specimens among species) in rivers, as noted by Patrick (1972).

Primitive Plants

Of the primary producers in rivers, algae are most important (Table 6; Patrick 1972). Some species are believed to have evolved within rivers (Hynes 1970); in fact, they appear to possess an "innate current demand", according to Benfield (1981). The many adaptations of lotic algae, including opportunistic growth (Benfield 1981), presumably allow their rapid recovery from setbacks such as reset mechanisms, or other periodic or episodic events discussed earlier. Hynes (1970) noted that the "epipelic" (mud dwelling) habits of some species enable them to retain their position within the stream. Others are "epilithic" (living on stones or similar objects) and thus, they anchor themselves via a stalk or a jelly-like substance. He also mentions that the thallus, another feature promoting algal stability, may be flattened so that a larger surface area is adherent to the substrate. Yet other species of algae are endowed with a cushion-like shape, which diverts water flow over them; or rhizoid-like structures at the bases of filaments, sometimes exceeding 1 m in length, to aid in anchoring algae to the substrate. Finally, higher respiratory rates are also important in lotic algal survival (Whitford and Schumacher 1961).

Bryophytes, and to a lesser degree lichens, are prevalent inhabitants of rivers. Hynes (1970) suggested that rocks in fast-flowing stream sections are the most common sites of moss growth. He noted that these primitive plants are shade tolerant, and that the turbulence actually facilitates their uptake of carbon dioxide. Thus, they are ideally suited for a lotic existence. Moreover, bryophytes do not appear to be adversely affected by scouring (Hynes 1970).

Aquatic Macrophytes

Hynes (1970) observed that rooted plants have no notable morphological adaptations to running water, aside from their tough, flexible stems and their creeping-growth habit (stolons, rhizomes, adventitious roots), which allow them to maintain their position on the stream bed. He noted that current-induced reductions in size, however, are commonly observed in rooted plants. The same plant species may vary markedly in appearance, depending on whether it is found in a lotic or a lentic environment, or whether it is exposed to or sheltered from the current. For example, the upstream and laterally-directed leaves found within a single clump of *Nuphar luteum* plants, may be more reduced than those which are protected from the current (Hynes 1970). Furthermore, certain plant types tend to be successful on particular substrate types. The lack of riverine adaptations may be a reflection of the recent glaciation in the north-temperate zone, which suggests that macrophytes may have been derived from lake habitat. Hynes (1970) found that the following are controlling factors in the success of rooted plants: 1) current speed; 2) water hardness; 3) the frequency of strong, sudden outbursts of water (i.e. flooding); 4) light; and 5) nutrients. In view of this, macrophytes contribute progressively more to the primary production in areas of low gradient and shallow water (Benfield 1981) and in regions where the above factors are not limiting.

Floating plants are relatively rare in north-temperate lotic environments; however, they assume a much greater importance in the tropics (Hynes 1970), where high levels of turbidity give them a competitive advantage over submerged plant species.

Lentic ecosystems differ from rivers in that they are characterized by more stable water levels, a factor favorable to aquatic macrophytes (Table 6). The water stability also eliminates the need

for algal anchoring to the substrate; consequently, lentic algae are predominantly pelagic. In the euphotic sector of the pelagic zone, algae can also capitalize on high levels of solar radiation. Standing waters, then, are more conducive to both phytoplankton (Welcomme 1979) and macrophyte growth. Mosses, while generally rare in lakes, are sometimes present where the euphotic zone intercepts the littoral zone.

FAUNA

Zooplankton

Faunal assemblages of certain stream sections have long been linked to the prevailing physical conditions (e.g. Adams 1901; Hynes 1970). Zooplankton growth, for example, is generally very slow in the main stem of a flood plain river due to the swiftness of flow, high turbidity levels, and low dissolved oxygen (Hynes 1970; Welcomme 1979). Nevertheless, the generally turbid, high order river is likely to contain more zooplankton than the low order reaches, due to the more lentic characteristics of the former, the periodic influxes of drift and plankton along the length of the river, and the resultant nutrient enhancement downstream.

Lakes tend to harbour a pelagic zooplankton community of relatively high stability and abundance. Here, the limiting factors common to the lotic environments (e.g. unidirectional flow, high turbidity) are not sufficiently great to represent the same severe growth restraints.

Invertebrates

Lotic invertebrates exhibit many types of adaptations to swift water. Some protection from the current is afforded them within the "boundary layer" (Table 7; Ambühl 1961), a layer of water a few millimeters in thickness, just above the substrate, where the current speed is considerably lessened and smooth flow results (Hynes 1970; Moss 1980). A flattened body has evolved in some species, as in the dorsally compressed mayflies (e.g. *Baetis* spp.), which allows them to lie flat and protected within the boundary layer, or crawl under stones for protection (Varley 1967; Moss 1980). Moss (1980) noted that some organisms use suckers to cling to rocks (e.g. snails and dipterans), while certain adaptive features, including small movable spines, hooks, grapples, and claw-like legs, allow various other species to maintain a foothold. Silk pads, functioning either as a receptacle for hooks or as an asylum for cocoons, are also spun by various species (Moss 1980). The longitudinal succession of species associations, as described for fishes (Huet 1959), is also in evidence for invertebrates (e.g. Varley 1967; Ward 1986).

While some invertebrates are unique to lotic ecosystems, numerous specializations for a limnetic existence occur as well (e.g. Hynes 1970; Pennak 1978). The absence of both continual, undirectional turbulent flow, and a boundary layer in lakes, remain two of the most conspicuous habitat differences between the two systems; hence, the lentic benthos component does not require numerous turbulence-related adaptations. While the water velocity appears to have a major influence on the abundance of riverine invertebrates, the production of bottom fauna in large deep lakes may be largely determined by morphometric conditions (Rawson 1953), substrate type, and dissolved oxygen levels.

Invertebrates are numerous in the headwaters of rivers, and as a result, predation is widespread there. Hynes (1970) discussed the great significance of invertebrates in the diets of most riverine fishes. Terrestrial insects are not as important in the diet of lake fishes; rather, forage fishes are consumed extensively by many lentic piscivores, while crustaceans and aquatic insects constitute another sizable prey component.

Fishes

An astounding variety of adaptations has developed for fishes in fluvial environments; presumably, this is due to the long-standing history of fishes' occurrence and evolution in rivers, especially in Europe (Balon et al. 1977). Fishes characteristic of turbulent waters are generally streamlined,

Table 7. A comparison of selected adaptive attributes of stream and lake fauna, especially as applied to the north-temperate zone.

Attribute	Rivers	Lakes
Zooplankton growth	Low; greatest in high or intermediate order streams; limited by turbidity	Considerable; limiting factors less significant
Boundary layer	Present, shelters benthic organisms	Absent
Invertebrate predominance	Headwaters	Littoral
Primary fish food	Invertebrates	Forage fishes
Typical morphological characteristics of fishes	Streamlined; round to oval in cross-section	Deep-bodied; laterally compressed
Adaptations of fishes	Numerous, adaptive to a turbulent, turbid environment	Numerous, adaptive to pelagic and bathypelagic conditions
Climatic stresses	Severe; extreme temperature fluctuations in summer; ice formations and near-freezing temperatures in winter	Moderate; limited by low levels of dissoved oxygen in winter
Production/biomass ratio	Increases downstream, maximum in 3rd to 5th order streams	Increases near shore

Data were derived, in part, from the following sources: Varley 1967; Hynes 1970; Welcomme 1979; Moss 1980; Moyle and Cech 1982; Ward 1985.

and round (or oval) in cross-section according to Varley (1967). In combination with the predominant red muscle (adaptive for sustained swimming power) of river fishes, such a shape facilitates movement upstream, enabling fishes to maintain their positions against the current. Other species may possess adhesive disks, or a dorso-ventrally flattened shape, with which they can counter the effects of current (Varley 1967). Alternatively, swimbladders may be absent in some stream fishes (Scott and Crossman 1973; Kuehne and Barbour 1983), as effective buoyancy regulation is not necessarily crucial to riverine fish existence.

Adaptations also exist among river fishes which facilitate movement in a nocturnal or turbid environment (Table 7; Ryder 1977). Frequently, these fishes possess a tapetum lucidum (e.g. Moore 1944), electrical organs (Lissman 1963), barbels, or an advanced acousticolateralis system (Alexander 1967). The eyes of river fishes may be dorsally oriented for optimum light gathering, or reduced as a protection against suspended particles.

Other riverine fish adaptations may range from air-breathing in slow-flowing flood plain rivers (Cummins 1972) to the subterminal, protuberant mouth of some river fishes, which is a convenient mechanism for scouring the bottom for food.

Welcomme (1979, 1985) identified two types of behaviourally distinct flood plain fishes. The first group, termed "whitefish", migrates to the main river channel when severe conditions in the flood plain render it necessary. "Blackfish", on the other hand, are

extremely tolerant of deoxygenated conditions (Welcomme 1979). Analogous to the African "whitefish" phenomenon in North America are the movements of fishes into the mouths of tributaries to avoid certain stress conditions, such as low dissolved oxygen (Gammon and Reidy 1981). Also, the seasonal migrations in northern Canada of chars (e.g. *Salvelinus alpinus*, *S. fontinalis*) from Hudson Bay into their natal streams, allow them to escape the inordinately low temperatures (circa -1.7°C) found in the estuarine environment during winter (e.g. Sprules 1952; Brett and Alderdice 1958).

Flood plain fishes may possess unusual and highly specialized adaptations. For example, Welcomme (1979) reported "upside-down" swimming positions (allowing effective browsing on submerged nearshore roots), burrowing in sandy substrates, serpentine shapes, and the small size of certain species. The two latter features facilitate movement through entangled vegetation, and enable fishes to hide within the vegetation.

The fishes of lentic, or slow-moving waters, may differ considerably in structure from those found in rivers. Lake fishes are typically deep-bodied and laterally flattened, or disk-shaped (Varley 1967). In accordance with a frequent pelagic existence, these fishes are often silvery, with relatively large, laterally oriented eyes. White muscle is the primary muscle type possessed by lake fishes; hence, many lentic species might not tolerate life in swift rivers, as they would not have the sustained energy resources necessary to withstand the current for long periods (Varley 1967). Swimbladders are almost essential as buoyancy regulators (except for certain demersal species such as the deepwater sculpin, *Myoxocephalus quadricornus*) in lentic waters, which are of a relatively great mean depth. In addition, the neuromast canals, so extensive and functional in a riverine stone loach (Cobitidae), are absent altogether in another loach that is an inhabitant of still water (Alexander 1967).

The lotic fish fauna must be adept at survival in a dynamic, seasonally variable habitat. In summer, the drastic hourly and diurnal temperature fluctuations probably represent a thermal stress to stream fishes (Brown 1969; Hynes 1970). Austere and rigorous winter conditions may pose an even greater threat to fish survival. For example, extreme water level and temperature fluctuations are quite common during winter, and the combined effects tend to stress trout. Inclement winter conditions may result in high fish mortality rates (e.g. 60%, on average, for trout in Convict Creek; Maciolek and Needham 1951; Reimers 1963). Therefore, a poor, post-winter body condition may often be attributed to excessive, temperature-induced catabolism (Reimers 1963). Hunt (1969) suggested that the warmer temperatures of Lawrence Creek, Wisconsin, were partially responsible for an enhanced overwinter survival rate, when compared with that of Convict Creek.

Despite its often adverse effects, winter represents a mixed blessing to stream biota. Maciolek and Needham (1951) noted, for example, that snow and ice may shield biota from both the cold and predators. Frazil ice seemed to alter stream morphology periodically, but there was no obvious sign of harm to the fishes on a short-term basis. In their winter study of Convict Creek, California, Maciolek and Needham (1951) revealed that while rapid increases in flow (sometimes doubling between early morning and noon) displaced many aquatic organisms, this proved to be of benefit to trout, which could feed more readily on riffle-dwelling insects.

Overwintering lake fish species are subjected to climatic stresses which vary somewhat from those in rivers. Ice may be a limiting factor in fish survival; however, this is largely in the sense that it prevents wind-activated aeration of the water, a major source of oxygen during ice-free seasons (Wetzel 1975). When dissolved oxygen levels are insufficient for respiration, a considerable "winterkill" of fishes may ensue (Greenbank 1945). In general, winter conditions in lakes (with the exception of dissolved oxygen insufficiency) are more benign than those in rivers and, therefore, less stressful to lentic biota.

Studies concerning lotic fish yields, particularly in north-temperate rivers, have been sorely neglected in the past. Yield measurement in warmwater streams, as elsewhere, has been plagued with difficulties, due to the mobility of both fish and fishermen in such lengthy, open-ended systems (Larimore 1981). In pioneering studies, however, Welcomme (e.g. 1976, 1979, 1985, 1988) correlated yields with water conductivity, river length, drainage basin area, and maximum flooded area in tropical flood plain rivers. Platts et al. (1983) suggested that a measure of stream width or mean depth would allow an estimate of fish standing stocks and biomass per unit area. Platts (1979) also suggested that the magnitude and frequency of orders in Idaho streams would provide general information on fish species present, as well as estimates of standing stocks within single planning units; however, this view is not shared by all workers (e.g. Hughes and Omernik 1981). In general, all work pertaining to definitive, quantitative measures of fish yields in lotic systems has, until recently, been directed towards moderately small streams.

Studies involving estimates of standing stocks, production and yield of lakes are legion and have been extensively documented (e.g. Ricker 1975; Bagenal 1978). Predictive models are sufficiently sound to be able to estimate total fish yields from large lakes and reservoirs with a satisfactory degree of precision for management purposes (e.g. Ryder 1978b).

FINAL INTEGRATION AND EVALUATION

Our stated intention within this paper is to examine the world's rivers within a lake ecology context (Thienemann 1953) and from an Ontario perspective; to identify areas of commonality and contrast between rivers and lakes (Table 8), where concepts and methodologies may be transferable from a comprehensive lake data base, to a deficient one for Ontario streams; and finally, to explore unifying concepts in ecology (van Dobben and Lowe-McConnell 1975) that will allow comparable approaches to the fisheries management of both lake and river eco-

Table 8. Some qualitative differences between rivers and lakes.

Qualitative differences	Rivers	Lakes
Major energy source	Detritus	Solar radiation
Nutrient regime	Spiralling	Cycling
Reset events	Floods (severe) Ice scouring	Overturn (moderate)
Fragility	Fragile; rapid recovery	Well buffered; slow recovery
Resilience	High	Low
Community structure	Sequential (seasonal), successional (spatial), mainly stochastic	Harmonic, successional (temporal), mainly deterministic
Community refugium	Boundary layer; hyporheic zone (i.e. deep inhabitable substrate)	Ecotone; shallow inhabitable substrate

Data were derived, in part, from the following sources: Hynes 1970; Cummins 1974; Webster 1975; Ryder and Kerr 1978; Vannote et al. 1980; Grossman et al. 1982; Holling 1985; Minshall et al. 1985.

systems (Regier and Henderson 1980). Accordingly, our level of comparison has been both restrictive and selective, rather than exhaustive, and we have sought to garner, synthesize, and comprehend the various insights included in the recent literature in preference to proffering new analyses of our own.

Our initial impression upon surveying a substantial part of the stream ecological literature of the recent past, has been the relatively large contribution made towards the understanding of these complex ecosystems by Vannote et al. (1980) through their River Continuum Concept. Their concepts have synthesized, clarified and generalized much of what was known about stream ecology until recently; a more topical contribution to the literature by Minshall et al. (1985) has crystallized the concept even further. The River Continuum Concept likely represents a new paradigm in the field of stream ecology in the sense of Kuhn (1962). As such, it is a convenient launching pad for future endeavours in Ontario that attempt to describe and quantify the aquatic biota of its streams and rivers, with a particular but practical bent towards the assessment of potential fish yields. The new synthesis of stream ecology provided by the River Continuum Concept and complemented by the comparative approach herein (river ecology vs lake ecology), would seem to provide a rapid entry into a complex and often controversial subject (e.g. Statzner and Higler 1985). Our further focus on stream ecology, from a broad lake perspective, will hopefully provide a common basis that will permit science transfer where appropriate, as recommended by Ricker (1934).

Our previous observations outlined similarities and differences between lakes and streams in a somewhat detailed, but non-exhaustive fashion. Now we wish to draw attention to certain commonalities of rivers and lakes through a more generalized "compare and contrast" exercise. On that basis, we will compare rivers and lakes from the perspective of a series of several pairs of dichotomies (Fig. 1-6). Each dichotomous pair is clinal in nature, and represents a gradient or continuum between two polar extremes. The gradient in each case is unlikely to be perfectly linear, although in certain instances linearity may be approached.

Each of our comparisons will be done from within a *caeteris paribus* context, and a somewhat arbitrary, or subjective point of view. Our casually derived constructs are intended to focus attention on important distinctions between lotic and lentic environments, and thereby provide an heuristic understanding of the similarities and differences between the two subsystems. Other observers may, with equal justification, make different distinctions.

Accordingly, our observation that rivers are horizontally oriented, while lakes have a vertical orientation, does not preclude the converse condition, nor does it fail to recognize that both orientations exist in each instance, but rather places emphasis on the following important ecological principle. Within an ecosystem, lakes provide a storage function (vertical orientation), whereas rivers form connecting links within a complex matrix, and are primarily vehicles for communication and transport (horizontal orientation).

SPACE-TIME ORGANIZATION

Most physical, chemical and biological phenomena in rivers are spatially organized (Fig. 1); that is, marked differences occur as the stream is traversed from headwaters to mouth. This spatial organization applies to ecological succession, nutrient inputs, production processes, stream velocity, dissolved solids concentrations, and the structure and function of lotic communities (e.g. Vannote et al. 1980). Many other natural phenomena in rivers are also structured horizontally in a clinal fashion, from headwaters to mouth.

Implicitly, a disturbance or human intervention at any point on a river system, such as a massive spill of contaminants, might be expected to have dire consequences on the stream reaches below the input, but have next to no effect upstream. While this spatial dependency augers ill for stream fragility, it might be equally considered as beneficial to stream

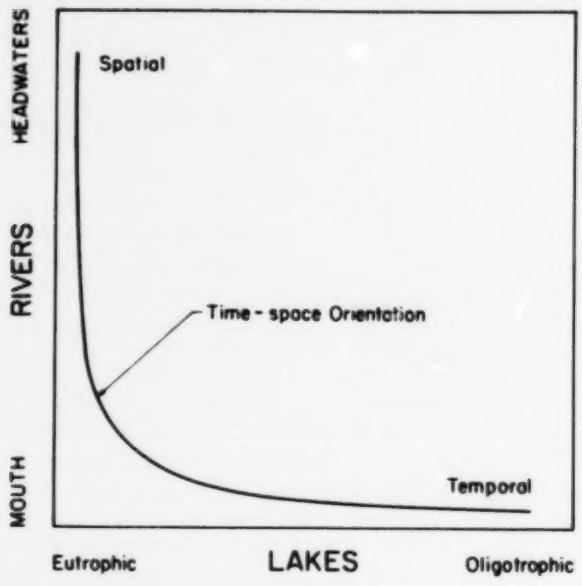

Fig. 1. Time-space orientation of rivers and lakes.

rehabilitation prognoses, especially to their inherent high level of resiliency (Table 8). Accordingly, a massive episodic spill of contaminants into a river system might be expected to be rapidly flushed downstream, and quickly replaced with water from the uncontaminated upper reaches, except for those toxic substances that may be trapped in organic bottom sediments or absorbed by the biota. Even there, floods during the spring spate, including accompanying ice-scouring, may cause toxic-laden sediments to be rapidly flushed out, at least on an annual basis.

Lakes, on the other hand, appear to be more temporally organized. Flushing rates (water renewal times) for lakes may vary from a few days to hundreds of years, depending on their volume and rates of inflow and outflow. Because of long water retention times with only moderate to slight horizontal movements of water (e.g. longshore currents), vertical density stratification commonly occurs for both heat and chemicals. Hence, a distinct and stable vertical regime is established twice each year in dimictic lakes for various physical, chemical, and biological processes and substances. In addition to thermal and chemical stratification, both dissolved oxygen and pH levels have pronounced vertical profiles (e.g. Hutchinson 1957). Production processes, such as photosynthesis, at the autotrophic or primary production level, generally take place in the upper trophogenic layer, while the lower, tropholytic layer may serve as a sink for organic matter produced in the upper zone (Wetzel 1975), as well as for heterotrophic activity. Hence, in general, the composite orientation and therefore, the organization of dimictic lakes of the north-temperate zone, appears to be based primarily on a vertical process and structural regime (Fig. 2), rather than on the horizontal regime found in rivers (Vannote et al. 1980). Nonetheless, when the hyporheic zone and current velocity stratification are considered, rivers have an important vertical dimension as well.

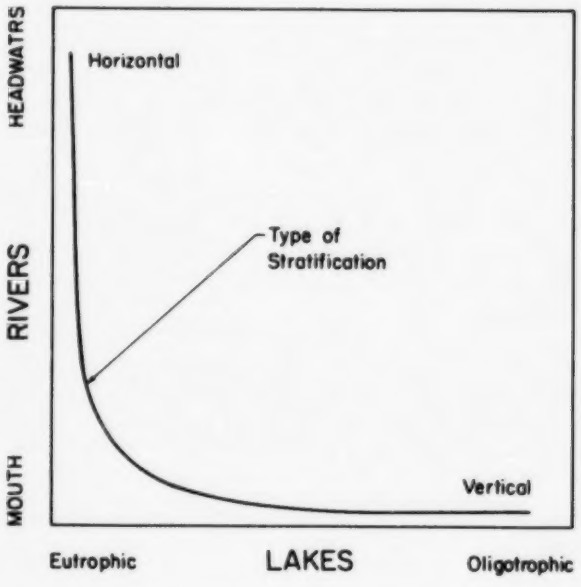

Fig. 2. Stratification plane of rivers and lakes.

Chemical contamination within a lake may not dissipate as rapidly as in rivers but, rather, may diminish over comparably lengthy periods of time depending on internal rates of dilution. The acute effect, however, is usually localized, with lesser, often undetect-

able effects occurring remote from the spill over longer time periods. Bottom sediments and biota may both be expected to absorb and retain certain contaminant loads over lengthy periods of time, giving up part of their burden to the water column during each overturn.

While space-time considerations and horizontal-vertical organization are not exclusive properties of either rivers or lakes, it is apparent that rivers and river processes, with their horizontal orientation, may be more readily analyzed on a spatial basis, while lakes with largely vertical regimes and structures, might best be addressed on a trend-through-time basis.

EXOGENOUS AND ENDOGENOUS EFFECTS

As a generality, forces external to the system tend to directly influence rivers more than lakes (Fig. 3), resulting in a more variable and unpredictable environment in the former (Sanders 1972). The morphology of rivers is subject to constant change through channel cutting, shore erosion and depositional processes. Weather has a large influence on water temperature, water levels, flow rates, and turbidity. As an example, stream water levels show instant response to summer rainstorms, an event of equal magnitude that may have only imperceptible effects on lake levels.

Lakes, in general, tend to have more stable properties over time, and much of this stability is derived from the buffering capacity of the biota. As the Gaia hypothesis (Lovelock 1979) presumes that life on earth controls atmospheric conditions, such that they are optimal for the biosphere (and hence biota), so does life in a lake provide feedback to the environment that results in the homeostatic regulation of a benign and favorable milieu for aquatic organisms. Hence, biological buffering is more prevalent in lakes than in rivers.

Both rivers and lakes derive energy and nutrients from within and from outside their immediate channels or basins (Fig. 4). The difference between these two aquatic systems is the relative proportion of nutrients and energy obtained from the two sources. Nutrient and energy sources, especially at the headwaters of a stream system, are largely allochthonous, that is, derived from allochthonous detritus (Hynes 1970), while for most lakes, autochthony, or

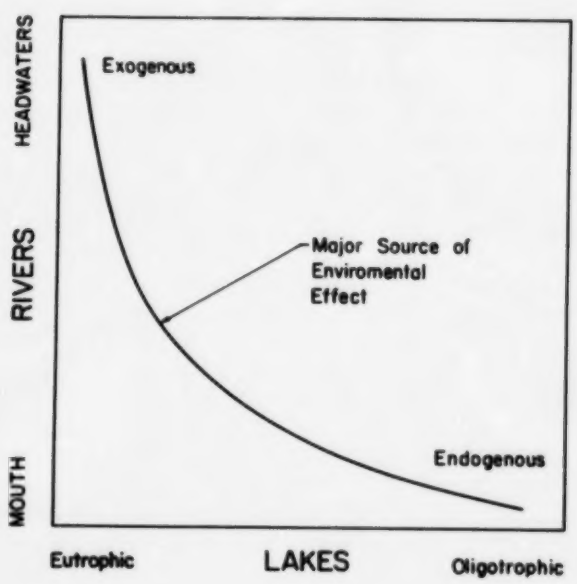

Fig. 3. Major source of environmental effects for rivers and lakes.

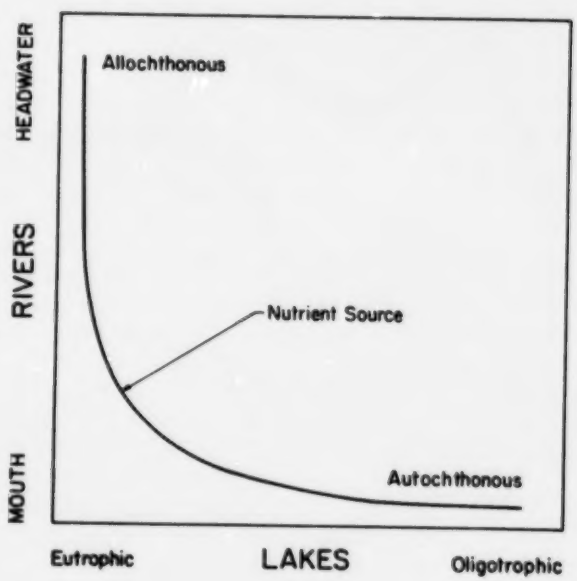

Fig. 4. Principal source of nutrients for rivers and lakes.

internal recycling, may account for a larger proportion of both energy and nutrients (Hutchinson 1957). The level of autochthony achieved by any particular lake is related to its trophic status. Hence, eutrophic lakes are more dependent upon allochthonous nutrient sources than are oligotrophic lakes.

While rivers and lakes constitute structurally different types of open systems, both are subjected to exogenous and endogenous effects to varying degrees including allochthonous and autochthonous sources of nutrients (Fig. 4). However, all things being equal, rivers are more immediately responsive to exogenous effects than are lakes. This derives from the fact perhaps, that rivers are *more* of an open system than are lakes, or alternatively, that lakes are closer to being true microcosms than are rivers (Forbes 1887).

ABIOTIC AND BIOTIC INFLUENCES

Rivers and lakes are subjected to different ecosystem controls derived from either abiotic or biotic sources (Fig. 5). As previously noted, rivers are more influenced by the vagaries of weather, and over the long term may be more closely attuned to climate than are lakes, especially thermally stratified, oligotrophic lakes. Rivers are also more responsive to their immediate geological and physiographic settings, and offer relatively little biological buffering to these influences when compared with lakes. This effect for streams is variable from headwaters to mouth as biological buffering increases downstream. Abiotic effects are proportionally greater on eutrophic lakes than on oligotrophic lakes, the latter of which owe a greater portion of their control to biotic effects. Extreme eutrophy, or hypereutrophy, has many of its biological processes curtailed because of the inordinately stressful nature of the abiotic effects (i.e. excessive phosphorous loadings).

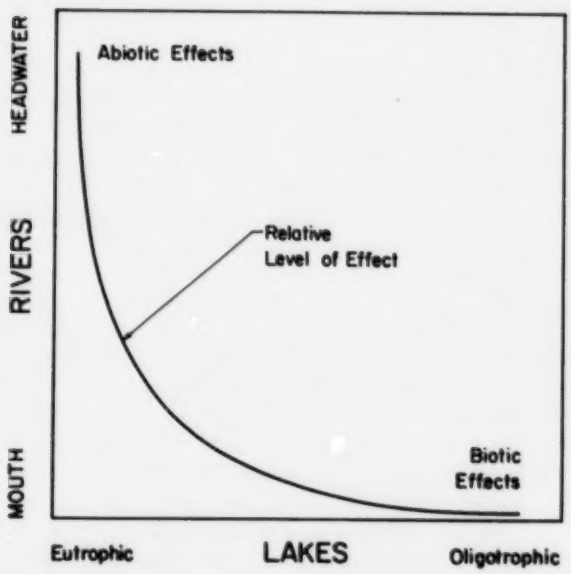

Fig. 5. Relative influence of biotic and abiotic effects in rivers and lakes.

The trophic cline in lakes, from oligotrophic to eutrophic, may also occur within a single river, normally with an augmentation of nutrients from headwaters to mouth. This gradual increase in the nutrient levels of a stream is not always predictable, as inflowing tributaries of lower nutrient levels could dilute substantially the nutrient levels in the mainstream (e.g. Ryder 1964). Nonetheless, as a generality it may be said that a river is more buffered biologically as it is traversed in a downstream direction, while lakes may be more biologically buffered in time, through oligotrophication processes.

As previously noted, the ratio of heterotrophy to autotrophy (H/A) in rivers varies as they are traversed from headwaters to mouth (Fig. 6). The highest H/A ratios occur in the shaded headwaters and the relatively turbid mouths of streams; there, solar insolation is reduced, and heterotrophic production becomes proportionately greater.

Lakes typically have the greatest levels of autotrophy in the upper trophogenic zone where solar light penetration is highest, and the lowest levels in the darker, tropholytic waters below. A more apt comparison with rivers on the basis of an H/A ratio may be made on a temporal scale for north-temperate lakes which have highest levels of photosynthesis during the long daylight hours of summer and lowest

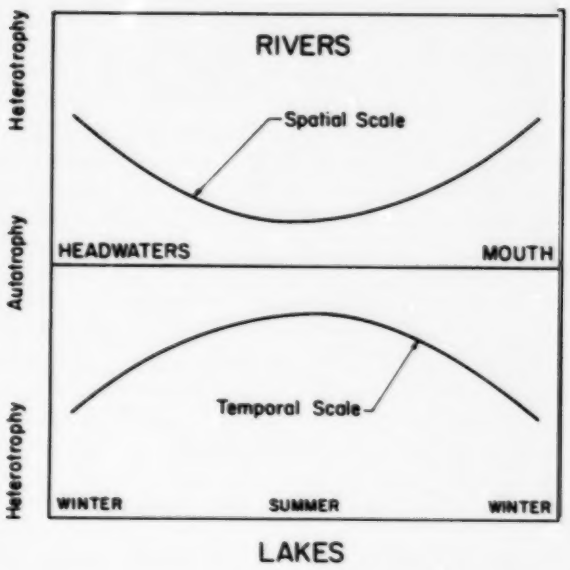

Fig. 6. Ratio of autotrophy to heterotrophy in rivers and lakes.

levels during the relatively short days of winter. The latter effect is accentuated through the presence of a thick layer of ice and snow over the surface of a lake at northerly latitudes. Accordingly, H/A ratios for lakes will be lowest in summer and highest during winter (Fig. 6).

COMMUNITY STRUCTURE

The structure of river and lake communities differ considerably, both in time and spatially. Studies of low-order streams have demonstrated that biotic communities in temperate regions may form "a temporal sequence of synchronized species replacement" (Vannote et al. 1980); however, this is not necessarily true of equatorial regimes (Statzner and Higler 1985). When species replacement occurs, each new species essentially fills the same ecological role as its predecessor, but is better adapted to some seasonal change in the microhabitat. The ecological consequence is an equitable distribution of energy over time, and an attendant maximization of resource use. Additionally, stream communities change spatially from headwaters to mouth, which in the case of benthos, is apparently a size-related dependency between the organism and its detrital food (Vannote et al. 1980).

The composition of culturally unperturbed lake communities, on the other hand, does not change markedly from season to season, although topological distortion of specific community compartments may occur with the addition of new cohorts. In general, lake communities tend to be more stable than stream communities over time, and variation occurs spatially rather than temporally. For example, it has been shown that percid communities have a habitat median of central tendency distinct from that of salmonid communities, even when both communities occur sympatrically in the same lake (Ryder and Kerr 1978). Usually one or more environmental parameters are sufficient for ecological separation of the two communities (e.g. Svärdson 1976); in the latter instance, temperature alone would seem to suffice, although phosphorous may also be important in this respect (Marshall and Ryan 1987).

On this basis then, community diversity might be expected to be highest in mesotrophic lakes where species from three distinct communities may find discrete areas of the lake best suited to their life requirements (Ryder and Kerr 1978; 1988). On a regional basis (the north-temperate zone, for example), maximum community diversity occurs in those medium to large lakes that combine the widest range of environmental conditions (Barbour and Brown 1974).

Similarly, maximum community diversity and primary production are generally greatest in streams of the third to fifth order, which are usually medium-sized streams occupying the mid-point of the sequence of stream order and having the widest range of temperature variation (Vannote et al. 1980; but see Statzner and Higler 1985).

TRANSFERABLE SCIENCE AND RESEARCH NEEDS

Certain aspects of lake ecology may be readily transferred to rivers to good advantage. Many phenomena that are temporal occurrences in lakes occur spatially in rivers from headwaters to mouth; where these are fundamental

ecosystem or community properties, such as production or diversity, appropriate insights may be gained from lake data sets for rivers within the same climatic zone. In fact, space-time axes may be profitably interchanged between rivers and lakes for various measurements, and in many applications. Application of erogodic theory (Ryder et al. 1974), that is, relating the means of temporal strings with those of spatial arrays, may be one approach useful for utilizing lake information within a river context. Such an approach for Ontario biologists would allow rapid transfer of ecological insights from lakes to rivers. It may also provide a directionality for future research on rivers, or at least be indicative of research needs.

In the latter area, the pragmatic need that is foremost in Ontario is the development of an ecologically sound, conceptual basis for the estimation of standing stocks and production of fishes in streams and rivers (Welcomme et al. 1988). An urgent requirement is to be timely with these estimates, rather than place an overemphasis on precision (e.g. Henderson et al. 1973). Accordingly, the development of a fish yield estimator for Ontario streams, on the same order of precision as the morphoedaphic index for lakes (Ryder et al. 1974), would be a first step towards effective management of river systems within the Province.

Because fish productivity in streams is so closely linked with the bordering terrestrial environment (Hynes 1963), an awareness of both the former pre-settlement conditions (Minshall et al. 1985) and appropriate conservation strategies for riparian zones and watersheds would be an additional asset to stream management.

Finally, despite our attempts to show where science may be transferred from lakes to rivers in a practical and meaningful manner, it should not be assumed that the transfer will be easily implemented without the appropriate background studies. Throughout this paper we have emphasized commonalities of rivers and lakes, but we have also stressed the importance of qualitative differences (Table 8). When all is said and done, a river exceeds the simple description of "a mobile lake", and a lake is something more than a "river reach, frozen in time". In dealing with these qualitative differences between rivers and lakes, much remains to be done.

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LITERATURE CITED

ADAMS, C. C. 1901. Base leveling and its faunal significance with illustrations from southeastern United States. Am. Nat. 35: 839-852.

ADAMS, G. F., and C. H. OLVER. 1977. Yield properties and structure of boreal percid communities in Ontario. J. Fish. Res. Board Can. 34: 1613-1625.

ALEXANDER, R. M. 1967. Functional design in fishes. Hutchinson Lib., London. 160 p.

ALI, M. A., R. A. RYDER, and M. ANCTIL. 1977. Photoreceptors and visual pigments as related to behavioural responses and preferred habitats of perches (*Perca* spp.) and pikeperches (*Stizostedion* spp.). J. Fish. Res. Board Can. 34: 1475-1480.

AMBÜHL, H. 1961. Die Strömung als physiologischer und ökologischer Faktor. Experimentelle Untersuchungen an Bachtieren. Verh. Int. Ver. Limnol. 14: 390-395.

BAGENAL, T. [ed.] 1978. Methods for assessment of fish production in fresh waters. IBP Handbook No. 3, Blackwell Sci. Publ., London. 365 p.

BALON, E. K., W. T. MOMOT, and H. A. REGIER. 1977. Reproductive guilds of percids: results of the paleogeographical history and ecological succession. J. Fish. Res. Board Can. 34: 1910-1921.

BARBOUR, C. D., and J. H. BROWN. 1974. Fish species diversity in lakes. Am. Nat. 108: 473-489.

BARTON, D. R., W. D. TAYLOR, and R. M. BIETTE. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. North Am. J. Fish. Manage. 5: 364-378.

BEAUMONT, P. 1975. Hydrology, p. 1-38. *In* B.A. Whitton [ed.] River ecology. Univ. California Press, Berkely, CA.

BENFIELD, E. F. 1981. Primary production in stream ecosystems, p. 82-90. *In* L.A. Krumholz [ed.] Warmwater Streams Symposium. Allen Press, Lawrence, KS.

BENSLEY, B. A. 1922. A plan for the biological investigation of the water areas of Ontario. Univ. Toronto Stud., Publ. Ont. Fish. Res. Lab. No. 1: 1-23.

BLUM, J. L. 1972. Plant ecology in flowing water, p. 53-56. *In* R.T. Oglesby, C.A. Carlson and J.A. McCann [ed.] River ecology and man. Academic Press, New York, NY.

BORNER, L. 1917. Die Bodenfauna des St. Moritzer - See. Inaugural Dissertation. Basel. Univ. Stuttgart. 163 p.

BRETT, J. R., and D. F. ALDERDICE. 1958. The resistance of cultured young chum and sockeye salmon to temperatures below 0°C. J. Fish. Res. Board Can. 15: 805-813.

BRINKHURST, R. O. 1974. The benthos of lakes. MacMillan Press, London, New York. 190 p.

BROWN, G. W. 1969. Predicting temperatures of small streams. Water Resour. Res. 5: 68-75.

CAIRNS, J., JR. 1968. Suspended solids standard for the protection of aquatic organisms. Purdue Univ. Eng. Bull. 129: 16-27.

CLEMENS, W. A. 1923. The limnology of Lake Nipigon. Univ. Toronto Stud., Publ. Ont. Fish. Res. Lab. No. 11: 1-31.

CORDONE, A. J., and D. W. KELLY. 1961. The influence of inorganic sediment on the aquatic life of streams. Calif. Fish Game 47: 189-228.

COUTANT, C. C. 1975. Responses of bass to natural and artificial temperature regimes, p. 272-285. *In* R.H. Stroud and H. Clepper [ed.]. Black bass biology and management. Sport Fish. Inst., Washington, DC.

COX, E. T. 1978. Counts and measurements of Ontario lakes. Ont. Min. Nat. Resour., Toronto. 114 p.

CUMMINS, K. W. 1972. What is a river? - A zoological description, p. 33-52. *In* R.T. Oglesby, C.A. Carlson and J.A. McCann [ed.] River ecology and man. Academic Press, New York, NY.

CUMMINS, K. W. 1974. Structure and function of stream ecosystems. Bioscience 24: 631-641.

CUMMINS, K. W. 1975. The importance of

different energy sources in freshwater ecosystems, p. 50-64. *In* Productivity of world ecosystems. Proc. Symp. Aug. 31-Sept. 1, 1972. Nat'l. Acad. Sci., Washington, DC.

CUMMINS, K. W. 1977. From headwater streams to rivers. Am. Biol. Teach. 39: 305-312.

CUMMINS, K. W., and M. J. KLUG. 1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst. 10: 147-172.

CUMMINS, K. W ., and G. L. SPENGLER. 1978. Stream ecosystems. Water Spectrum Fall: 1-9.

CUMMINS, K. W., G. W. MINSHALL, J. R. SEDELL, C. E. CUSHING, and R. C. PETERSON. 1984. Stream ecosystem theory. Verh. Int. Ver. Limnol. 22: 1818-1827.

CUSHING, C. E. 1966. Periphyton productivity and radionuclide accumulation in the Columbia River, Washington, U.S.A. Hydrobiologia 29: 125-139.

CUSHING, C. E., C. D. McINTIRE, K. W. CUMMINS, G. W. MINSHALL, R. C. PETERSEN, J. R. SEDELL, and R. L. VANNOTE. 1983. Relationships among chemical, physical, and biological indices along river continua based on multivariate analyses. Arch. Hydrobiol. 98: 317-326.

DARLINGTON, P. J. 1957. Zoogeography: The geographical distribution of animals. John Wiley and Sons, Inc., New York, NY. 675 p.

DILLON, P. J., and F. H. RIGLER. 1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. J. Fish. Res. Board Can. 32: 1519-1531.

DISSMEYER, G. E. 1976. Erosion and sediment from forest land uses, management practices and disturbances in the southeastern United States. Proc. Third Federal Inter-Agency Sedimentation Conference, Sedimentation Committee, Water Resources Council, Denver, CO. Chap.1: 140-148.

DOAN, K. H. 1941. Relation of sauger catch to turbidity in Lake Erie. Ohio J. Sci. 41: 449-452.

DOUGLAS, B. 1958. The ecology of attached diatoms and other algae in a small stony stream. J. Ecol. 46: 295-322.

DYMOND, J. R. 1926. The fishes of Lake Nipigon. Univ. Toronto Stud., Publ. Ont. Fish. Res. Lab. No. 27: 1-108 + plates.

ELLIS, M. M. 1936. Erosion silt as a factor in aquatic environments. Ecology 17: 29-42.

FERNANDO, C. H. 1980. Tropical man-made lakes, African fish and cheap protein. ICLARM Newslet. 3: 15-17.

FORBES, S. T. 1887. The lake as a microcosm. Bull. Peoria Sci. Assoc. 1887: 77-87.

FRANCIS, G. R., A. P. L. GRIMA, H. A. Regier, and T. H. WHILLANS. 1985. A prospectus for the management of the Long Point ecosystem. Great Lakes Fish. Comm. Tech. Rep. No. 43. 109 p.

FRY, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser. No. 55, Publ. Ont. Fish. Res. Lab. 68: 1-62.

FUNK, J. L. 1970. Warmwater streams, p. 141-152. *In* N.G. Benson [ed.]. A century of fisheries in North America. Am. Fish. Soc. Spec. Publ. No. 7.

GAMMON, J. R., and J. M. REIDY. 1981. The role of tributaries during an episode of low dissolved oxygen in the Wabash River, Indiana, p. 396-407. *In* L.A. Krumholz [ed.] The Warmwater Streams Symposium. Allen Press, Lawrence, KS.

GIBBS, R. J. 1970. Mechanisms controlling world water chemistry. Science 170: 1088-1090.

GREENBANK, J. 1945. Limnological conditions in ice-covered lakes, especially as related to winter-kill of fish. Ecol. Monogr. 15: 344-392.

GROSSMAN, G. D., P. B. MOYLE, and J. O. WHITTAKER, JR. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. Am. Nat. 120: 423-454.

HALLAM, J. C. 1959. Habitat and associated fauna of four species of fish in Ontario streams. J. Fish. Res. Board Can. 16: 147-173.

HASLAM, S. M. 1978. River plants (The macrophytic vegetation of watercourses). Cambridge Univ. Press, New York, NY. 396 p.

HAWKES, H. A. 1975. River zonation and classification, p. 312-374. *In* B.A. Whitton [ed.] River Ecology. Vol. 2, Univ. California Press, Berkeley, CA.

HAYES, F. R. 1957. On the variation in bottom fauna and fish yield in relation to trophic level and lake dimensions. J. Fish. Res. Board Can. 14: 1-32.

HENDERSON, H. F., R. A. RYDER, and A. W. KUDHONGANIA. 1973. Assessing fishery potentials of lakes and reservoirs. J. Fish. Res. Board Can. 30: 2000-2009.

HOCUTT, C. H., and J. R. STAUFFER. 1975. Influence of gradient on the distribution of fishes in Conowingo Creek, Maryland and Pennsylvania. Chesapeake Sci. 16: 143-147.

HOLLING, C. S. 1985. Resilience of ecosystems: local surprise and global change, p. 228-269. *In* T.F. Malone and J. G. Roederer [ed.] Proc. Symp. ICSU, 20th Gen. Assembly. Cambridge Univ. Press, London.

HORTON, R. E. 1945. Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology. Bull. Geol. Soc. Am. 56: 275-370.

HUET, M. 1946. Note préliminaire sur les relations entre la pente et les populations piscicoles des eaux courantes. Règle des pentes. 13e Biologisch Jaarboek, Dodanaea, Bruxelles, p. 232-243.

HUET, M. 1949. Aperçu des relations entre la pente et les populations piscicoles des eaux courantes. Revue Suisse Hydrol. 11: 332-351.

HUET, M. 1959. Profiles and biology of western European streams as related to fish management. Trans. Am. Fish. Soc. 88: 155-163.

HUGHES, R. M., and J. M. OMERNIK. 1981. Use and misuse of the terms watershed and stream order, p. 320-326. *In* L.A. Krumholz [ed.] Warmwater Streams Symposium. Allen Press, Lawrence, KS.

HUNT, R. L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. J. Fish. Res. Board Can. 26: 1473-1483.

HUTCHINSON, G. E. 1957. A treatise on limnology. Vol. 1. John Wiley and Sons, New York. 1015 p.

HUTCHINSON, G. E. 1961. The paradox of the plankton. Am. Nat. 95: 137-145.

HUTCHINSON, G. E. 1967. A treatise on limnology. Vol. II. John Wiley and Sons, New York. 1115 p.

HUTCHINSON, G. E. 1975. A treatise on limnology. Vol. III. John Wiley and Sons, New York. 660 p.

HYNES, H. B. N. 1963. Imported organic matter and secondary productivity in streams. Proc. XVI Int. Congr. Zool. 4: 324-329.

HYNES, H. B. N. 1970. The ecology of running waters. Univ. Toronto Press, Toronto, ON. 555 p.

HYNES, H. B. N. 1975. The stream and its valley. Verh. Int. Ver. Limnol. 19: 1-15.

IWAMOTO, R. N., E. O. SALO, M. A. MADEJ, and R. L. McCOMAS. 1978. Sediment and water quality: a review of the literature including suggested approach for water quality criteria. U.S. Environ. Prot. Agency EPA 910/9-78-048 Washington, DC.

JONES, J. G. 1975. Heterotrophic microorganisms and their activity, p. 141-154. *In* B.A. Whitton [ed.] River

ecology. Univ. California Press, Berkely, CA.

KEREKES, J. 1976. Index of lake basin permanence. Int. Rev. Gesamten Hydrobiol. 62: 291-293.

KERR, S. R., and R. A. RYDER. 1988. The applicability of fish yield indices in freshwater and marine ecosystems. Limnol. Oceanogr. Spec. Iss.

KITCHELL, J. F., M. G. JOHNSON, C. K. MINNS, K. H. LOFTUS, L. GREIG, and C. H. OLVER. 1977. Percid habitat: The river analogy. J. Fish. Res. Board Can. 34: 1936-1940.

KUEHNE, R. A., and R. W. BARBOUR. 1983. The American Darters. Kentucky Univ. Press, Lexington, KY. 177 p.

KUHN, T. S. 1962. The structure of scientific revolutions. Foundations of the Unity of Sci. 11: 1-210.

LARIMORE, R. W. 1981. Progress and challenges of the fishery biologist in warmwater stream investigations, p. 120-126. *In* L.A. Krumholz [ed.] Warmwater Streams Symposium. Allen Press, Lawrence, KS.

LEOPOLD, L. B. 1953. Downstream change of velocity in rivers. Am. J. Sci. 251: 606-624.

LEOPOLD, L. B., and W. B. LANGBEIN. 1966. River meanders. Sci. Am. 214: 60-70.

LEOPOLD, L. B., M. B. WOLMAN, and J. P. MILLER. 1964. Fluvial processes in geomorphology. W.H. Freeman and Co., San Francisco. 522 p.

LISSMAN, H. W. 1963. Electric location in fishes. Sci. Am. 152: 1-12.

LOVELOCK, J. E. 1979. Gaia: a new look at life on Earth. Oxford Univ. Press, Oxford, UK. 157 p.

MACAN, T. T. 1961. A review of running water studies. Verh. Int. Ver. Limnol. 14: 587-602.

MacARTHUR, R. H. 1972. Geographical ecology. Harper and Row, New York. 269 p.

MACIOLEK, J. A., and P. R. NEEDHAM. 1951. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California, 1951. Trans. Am. Fish. Soc. 81: 202-217.

MARGALEF, R. 1960. Ideas for a synthetic approach to the ecology of running waters. Int. Rev. Gesamten Hydrobiol. 45: 133-153.

MARSHALL, T. R., and P. A. RYAN. 1987. Pattern analysis of fish associations in relation to environmental variables in northwestern Ontario lakes. Can. J. Fish. Aquat. Sci. 44 (suppl. 2): 198-215.

MARTIN, N. V. 1957. Reproduction of lake trout in Algonquin Park, Ontario. Trans. Am. Fish. Soc. 86: 231-244.

MARTIN, N. V. and C. H. OLVER. 1976. The distribution and characteristics of Ontario lake trout lakes. Ont. Min. Nat. Resour. Res. Rep. (Fish.) 97. 30 p.

McCOMBIE, A. M. 1959. Some relations between air temperatures and the surface water temperature of lakes. Limnol. Oceanog. 4: 252-258.

McINTIRE, C. D. 1975. Periphyton assemblages in laboratory streams, p. 403-430. *In* B.A. Whitton [ed.] River ecology. Univ. California Press, Los Angeles, CA.

MILBRINK, G. 1969. Microgradients at the mud-water interface. Inst. Freshwater Res. Drottningholm Rep. 49: 129-148.

MINCKLEY, W. L. 1963. The ecology of a spring stream Doe Run, Meade County, Kentucky. Wildl. Monogr. 11: 1-124.

MINSHALL, G. W., K. W. CUMMINS, R. C. PETERSEN, C. E. CUSHING, D. A. BRUNS, J. R. SEDELL, and R. L. VANNOTE. 1985. Developments in stream ecosystem theory. Can. J. Fish. Aquat. Sci. 42: 1045-1055.

MOON, H. P. 1939. Aspects of the ecology of aquatic insects. Trans. Br. Entomol. Soc. 6: 39-49.

MOORE, G. A. 1944. The retinae of two North American teleosts, with special reference to their tapeta lucida. J. Comp. Neurol. 80: 369-379.

MORTIMER, C. H. 1971. Chemical exchanges between sediments and water in the Great Lakes - speculations on probable regulatory mechanisms. Limnol. Oceanogr. 16: 387-404.

MOSS, B. 1980. Ecology of fresh waters. John Wiley and Sons, Toronto. 332 p.

MOYLE, P. B., and J. J. CECH, JR. 1982. Fishes: An introduction to ichthyology. Prentice-Hall, Inc., Englewood Cliffs, NJ. 593 p.

MOYLE, P. B., and B. VONDRACEK. 1985. Persistence and structure of the fish assemblage in a small California stream. Ecology 66: 1-13.

MÜLLER, K. 1974. Stream drift as a chronobiological phenomenon in running water ecosystems. Ann. Rev. Ecol. Syst. 5: 309-323.

MUNDY, P. R., and H. T. BOSCHUNG. 1981. An analysis of the distribution of lotic fishes with application to fisheries management, p. 266-275. *In* L. A. Krumholz [ed.] Warmwater Streams Symposium. Allen Press, Lawrence, KS.

NEEL, J. K. 1951. Interrelations of certain physical and chemical features in a headwater limestone stream. Ecology 32: 368-391.

NELSON, D. J., and C. C. SCOTT. 1962. Role of detritus in the productivity of a rock-outcrop community in a Piedmont stream. Limnol. Oceanogr. 3: 396-413.

NELSON, J. S. 1976. Fishes of the World. John Wiley and Sons, New York, NY. 416 p.

NIKOLSKY, G. V. 1963. The ecology of fishes. Academic Press, New York, NY. 352 p.

ODUM, E. P. 1971. Fundamentals of ecology. W.B. Saunders Co., Philadelphia, PA. 574 p.

ODUM, H. 1956. Primary production in flowing waters. Limnol. Oceanogr. 1: 102-117.

ORGHIDAN, T. 1959. Ein neuer Lebensraum des unterirdischen Wassers: Der hyporheische Biotop. Arch. Hydrobiol. 55: 392-414.

PATRICK, R. 1969. A proposed biological measure of stream conditions based on a survey of the Conestoga Basin, Lancaster County, Pennsylvania. Proc. Acad. Nat. Sci. Phila. 101: 277-341.

PATRICK, R. 1972. Commentary, p. 67-74. *In* R.T. Oglesby, C.A. Carlson and J.A. McCann [ed.] River ecology and man. Academic Press, New York, NY.

PENNAK, R. W. 1978. Fresh-water invertebrates of the United States (Second Edition). John Wiley and Sons, Toronto. 803 p.

PENNAK, R. W., and J. V. WARD. 1986. Interstitial faunal communities of the hyporheic and adjacent groundwater biotopes of a Colorado mountain stream. Arch. Hydrobiol./Suppl. 74. 3: 356-396.

PLATTS, W. S. 1979. Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho River drainage. Fisheries 2: 5-9.

PLATTS, W. S., W. F. MEGAHAN, and G. W. MINSHALL. 1983. Methods for evaluating stream, riparian and biotic conditions. Gen. Tech. Rep. INT-138. Ogden, Utah: U.S.Dep. Agricul., Forest Serv., Intermountain Forest and Range Experiment Sta. 1983. 70 p.

PUGSLEY, C. W., and H. B. N. HYNES. 1986. Three-dimensional distribution of winter stonefly nymphs, *Allocapnia pygmaea*, within the substrate of a southern Ontario river. Can. J. Fish. Aquat. Sci. 43: 1812-1817.

RAWSON, D. S. 1952. Mean depth and the fish production of large lakes. Ecology 33: 513-521.

RAWSON, D. S. 1953. The bottom fauna of Great Slave Lake. J. Fish. Res. Board Can. 10: 487-520.

RAWSON, D.S. 1960. A limnological comparison of twelve large lakes in northern Saskatchewan. Limnol. Oceanogr. 5: 195-211.

REGIER, H. A., and H. F. HENDERSON [ed.]. 1980. Comparative studies on freshwater fisheries. FAO Fish. Tech. Pap. No. 198. 46 p.

REID, G. K. 1961. Ecology of inland waters and estuaries. Reinhold Publ. Corp., New York, NY. 375 p.

REIMERS, N. 1963. Body condition, water temperature, and over-winter survival of hatchery-reared trout in Convict Creek, California. Trans. Am. Fish. Soc. 92: 39-45.

RICKER, W. E. 1934. An ecological classification of certain Ontario streams. Univ. Toronto Stud., Publ. Ont. Fish. Res. Lab. No. 49: 1-114.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. J. Fish. Res. Board Can. Bull. 191: 382 p.

RYAN, P. A., and T. R. MARSHALL (in prep.). Habitat suitability models for lake trout: the prediction of temperature and oxygen constraints.

RYCK, F., JR. 1975. The effect of scouring floods on the benthos of Big Buffalo Creek, Missouri. Proc. 29th Annu. Conf. Southeast Assoc. Game Fish Comm. 29: 36-45.

RYDER, R. A. 1964. Chemical characteristics of Ontario lakes as related to glacial history. Trans. Am. Fish. Soc. 93: 260-268.

RYDER, R. A. 1977. Effects of ambient light variations on behavior of yearling, subadult, and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34: 1481-1491.

RYDER, R. A. 1978a. Ecological heterogeneity between north-temperate reservoirs and glacial lake systems due to differing succession rates and cultural uses. Verh. Int. Ver. Limnol. 20: 1568-1574.

RYDER, R. A. 1978b. Fish yield assessment of large lakes and reservoirs - a prelude to management, p. 403-423. *In* S.D. Gerking [ed.] Ecology of freshwater fish production. John Wiley and Sons, New York, NY.

RYDER, R. A., and S. R. KERR. 1978. The adult walleye in the percid community - a niche definition based on feeding behavior and food specificity, p. 39-51. *In* R.L. Kendall [ed.] Selected coolwater fishes of North America. Am. Fish. Soc. Spec. Publ. No. 11. 437 p.

RYDER, R. A., and S. R. KERR. 1988. Harmonic communities in aquatic ecosystems: a management perspective, p. 00-00. Symposium on management schemes for inland fisheries. European Inland Fish. Advis. Comm. (EIFAC) XV/88/ Symp.1. Goteborg, Sweden. (In press)

RYDER, R. A., S. R. KERR, K. H. LOFTUS, and H. A. REGIER. 1974. The morpho-edaphic index, a fish yield estimator - review and evaluation. J. Fish. Res. Board Can. 31: 663-688.

RYDER, R. A., and J. PESENDORFER. 1988. Large rivers are more than flowing lakes: a comparative review, p. 00-00. *In* D.P. Dodge [ed.] Proc. Int. Large River Symp., Can. Spec. Publ. Fish. Aquat. Sci. 99. (In press)

SANDERS, W. M., III. 1972. Nutrients, p. 389-415. *In* R.T. Oglesby, C.A. Carlson, and J.A. McCann [ed.] River ecology and man. Academic Press, New York, NY.

SCHINDLER, D. W. 1977. Evaluation of phosphorus limitation in lakes. Science 195: 260-262.

SCHINDLER, D. W., and J. E. NIGHSWANDER. 1970. Nutrient supply and primary production in Clear Lake, eastern Ontario. J. Fish. Res. Board Can. 27: 2009-2036.

SCHLOSSER, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology 66: 1484-1490.

SCHMITZ, W. 1954. Grundlagen der Untersuchung der Temperaturverhaltnisse in den Fliessgewassern. Berl. Limnol. Flusstat. Freudenthal 6: 29-50.

SCOTT, W. B., and E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184. 966 p.

SEDELL, J. R., and J. L. FROGGATT. 1984. Importance of streamside forests to larger rivers: the isolation of the Willamette River, Oregon, U.S.A., from its flood plain by snagging and streamside forest removal. Verh. Int. Ver. Limnol. 22: 1828-1834.

SEDELL, J. R., and J. E. RICHEY. 1988. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers?, p. 00-00. *In* D.P. Dodge [ed.] Proc. Int. Large River Symp., Can. Spec. Publ. Fish. Aquat. Sci. 99. (In press)

SEEGRIST, D. W., and R. GARD. 1972. Effects of floods on trout in Sagehen Creek, California. Trans. Am. Fish. Soc. 101: 478-482.

SHELFORD, V. E. 1914. An experimental study of the behaviour agreement among animals of an animal community. Biol. Bull. 26: 294-315.

SHELFORD, V. E., and S. EDDY. 1929. Methods for the study of stream communities. Ecology 10: 383-392.

SMITH, R. L. 1980. Ecology and field biology (3rd ed.). Harper and Row, New York, NY. 835 p.

SPEAKER, R., K. MOORE, and S. GREGORY. 1984. Analysis of the process of retention of organic matter in stream ecosystems. Verh. Int. Ver. Limnol. 22: 1835-1841.

SPRULES, W. M. 1947. A management program for goldeye (*Amphiodon alosoides*) in Manitoba's marsh regions. Can. Fish Cult. II: 9-11.

SPRULES, W. M. 1952. The Arctic char on the west coast of Hudson Bay. J. Fish. Res. Board Can. 9: 1-15.

STANDORD, J. A., and A. R. GAUFIN. 1974. Hyporheic communities of two Montana rivers. Science 185: 700-702.

STATZNER, B., and B. HIGLER. 1985. Questions and comments on the River Continuum Concept. Can. J. Fish. Aquat. Sci. 42: 1038-1044.

STRAHLER, A. N. 1957. Quantitative analysis of watershed morphology. Trans. Am. Geophys. Union. 38: 913-920.

STUMM, W., and J. J. MORGAN. 1970. Aquatic chemistry - an introduction emphasizing chemical equilibria in natural waters. Wiley-Interscience, Toronto. 583 p.

SUMNER, W. T., and S. G. FISHER. 1979. Periphyton production in Fort River, Massachusetts. Freshwater Biol. 9: 205-212.

SVÄRDSON, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Inst. Freshwater Res. Drottningholm Rep. 55: 144-171.

THIENEMANN, A. 1953. Fluss und See, ein limnologischer Vergleich. Gewässer und Abwässer 1: 13-30.

TRISKA, F. J. 1984. Role of wood debris in modifying channel geomorphology and riparian areas of a large lowland river under pristine conditions: a historical case study. Verh. Int. Ver. Limnol. 22: 1876-1892.

VALLENTYNE, J. R. 1972. Freshwater supplies and pollution: effects of the demophoric explosion on water and man, p. 181-211. *In* N. Polunin [ed.] The environmental future. Macmillan Press, London.

VAN DOBBEN, W. H., and R. H. LOWE-McCONNELL [ed.]. 1975. Unifying concepts in ecology. First Int. Congr. Ecol., The Hague, The Netherlands. 302 p.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, and C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130-137.

VARLEY, M. E. 1967. British freshwater fishes (factors affecting their distribution). Fishing News (Books) Ltd. London, England. 148 p.

WALLACE, J. B., J. R. WEBSTER, and W. R. WOODALL. 1977. The role of filter feeders in flowing waters. Arch. Hydrobiol. 79: 506-532.

WALLEN, I. E. 1951. The direct effect of turbidity on fishes. Okla. Agric. Mech. Coll. Biol. Ser. 48: 1-27.

WARD, J. V. 1985. Thermal characteristics of running waters. Hydrobiologia 125: 31-46.

WARD, J. V. 1986. Attitudinal zonation in a Rocky Mountain stream. Arch. Hydrobiol. Suppl. 74: 133-199.

WARD, J. V., and J. A. STANFORD. 1988. Riverine ecosystems: the influence of man on catchment dynamics and fish ecology, p. 00-00. *In* D.P. Dodge [ed.] Proc. Int. Large River Symp., Can. Spec. Publ. Fish. Aquat. Sci. 99. (In press)

WATERS, T. F. 1969. Invertebrate drift-ecology and significance to stream fishes, p. 121-134. *In* T.G. Northcote [ed.] Symp. on salmon and trout in streams. H.R. MacMillan Lectures in Fish., Inst. Fish., Univ. British Columbia, Vancouver, BC.

WEBSTER, J. R. 1975. Analysis of potassium and calcium dynamics in stream ecosystems on three southern Appalachian watersheds of contrasting vegetation. Ph.D. Dissertation, Univ. Georgia, Athens, GA. 232 p.

WELCH, P. S. 1952. Limnology. McGraw-Hill Co., Toronto. 538 p.

WELCOMME, R. L. 1976. Some general and theoretical considerations on the fish yield of African rivers. J. Fish. Biol. 8: 351-364.

WELCOMME, R. L. 1979. Fisheries ecology of flood plain rivers. Longman Group Ltd., London. 317 p.

WELCOMME, R. L. 1985. River fisheries. FAO Fish. Tech. Pap. 262. 330 p.

WELCOMME, R. L. 1988. Review of the present state of knowledge of fish stocks and fisheries of African rivers, p. 00-00. *In* D.P. Dodge [ed.] Proc. Int. Large River Symp., Can. Spec. Publ. Fish. Aquat. Sci. 99. (In press)

WELCOMME, R. L., R. A. RYDER, and J. R. SEDELL. 1988. Dynamics of fish assemblages in river systems - a synthesis, p. 00-00. *In* D.P. Dodge [ed.] Proc. Int. Large River Symp., Can. Spec. Publ. Fish. Aquat. Sci. 99. (In press)

WETZEL, R. G. 1975. Limnology. W.B. Saunders Co., Philadelphia, PA. 743 p.

WHITFORD, L. A., and G. J. SCHUMACHER. 1961. Effect of current on mineral uptake and respiration by a freshwater alga. Limnol. Oceanogr. 6: 423-425.

WINGER, P. V. 1981. Physical and chemical characteristics of warmwater streams: a review, p. 32-44. *In* L.A. Krumholz [ed.] Warmwater Streams Symposium. Allen Press, Lawrence, KS.

WRIGHT, R. R. 1892. Preliminary report on the fish and fisheries of Ontario. Ont. Game Fish. Comm., Toronto, ON. p. 421-428.

YAKUWA, I. 1960. Phase of the diurnal variation of water temperature of a river. Mem. Eng. Fac. Hokkaido Univ. 11: 1-10.

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